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A General Fishery Model for a Size-Structured Fish Population

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Schnute, J. 1987. A general fishery model for a size-structured fish population. Can. J. Fish. Aquat. Sci. 44: 924–940.

This paper describes a fishery model based on size, rather than age, as the fundamental population variable. The model's key ingredient is a density function related to numbers of fish within any given size range. A key assumption is that selectivity in the fishery is determined by size, not age, and that fish can reach recruitment size at various ages. The theory easily yields moment equations comparable with those obtained recently by Fournier and Doonan; for example, the general moment equation here is derived in a four-line proof. The paper gives detailed recommendations for tailoring the new model to a specific fishery, where model complexity is determined by the available data. The new theory places earlier models of Deriso and Schnute in the context of generalized cohort analysis, where size-dependent mortality is allowed. In particular, the paper identifies a potential problem with these earlier models and proposes a solution. All results are interpreted biologically to provide both conceptual and analytical tools for stock assessment.

L'auteur présente un modèle des pêches basé sur la taille plutôt que sur l'âge comme principale variable de la population. La composante clé du modèle est une fonction de densité liée au nombre de poissons au sein d'une gamme de tailles donnée. L'une des principales hypothèses est que la sélectivité de la pêche est déterminée par la taille, non par l'âge, et que les poissons peuvent atteindre la taille de recrutement à divers âges. Cette théorie permet facilement d'obtenir des équations de moments comparables à celles récemment obtenues par Fournier et Doonan. Ainsi, une preuve de quatre lignes suffit à obtenir l'équation générale du moment. L'auteur présente des recommandations détaillées pour l'ajustement du nouveau modèle à une pêche précise, la complexité du modèle étant déterminée par les données disponibles. Cette nouvelle théorie situe les modèles antérieurs de Deriso et Schnute dans le contexte de l'analyse généralisée des cohortes qui autorise une mortalité dépendante de la taille. Plus particulièrement, l'auteur souligne le problème que peuvent poser ces modèles antérieurs et propose une solution. Tous les résultats sont interprétés de façon biologique afin d'obtenir des outils tant conceptuels qu'analytiques pour l'évaluation des stocks.

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Recent research has established a mathematical relationship between difference equations directly associated with fishery data and more detailed underlying biological models (Deriso 1980; Schnute 1985; Fournier and Doonan 1987). The object of all this work is to make the link between biology and theory as precise as possible. Unfortunately, from a practical point of view, the theory becomes increasingly complex as more complex biological processes are included in the underlying model. Furthermore, there is even some debate as to the degree of complexity that is useful (Ludwig and Walters 1985).

The simplest model, described by Deriso (1980) and Schnute (1985), is based on the assumption that the fishery has "knife-edged" selectivity. This means that, for some fixed age k, fish of age k or older experience uniform fishing mortality, while fish younger than k are invulnerable to the fishery. There are two unfortunate consequences of this assumption. First, it clearly is too simplistic. For example, if the fishery is managed with a size limit, fish may reach the critical size at various ages. Second, on the analytic side, the assumption forces the modeler to make a fixed choice for k. This fixes the time lag between spawning and recruitment and gives the difference equation a specific structure. In particular, that structure does not include a general autoregressive process in which the current state is allowed to depend on an arbitrary number of earlier states.

Two recent papers have helped resolve the limitations of the simple model described above. First, Fournier and Doonan (1987) placed the model in a much broader context of models containing groups of fish with varying susceptibility to the fishery. Their approach generalizes an earlier "incomplete recruitment" model proposed by Deriso (1980). They obtained a very general set of difference equations for such models and showed that their methods apply to wide range of data when available, such as mean weights and mean square weights from fish samples. In essence, Fournier and Doonan derived difference equations for arbitrarily high-order moments of the population's size distribution. Just as the mean, standard deviation, skewness, and kurtosis are useful characteristics of a statistical distribution, so too they may be informative measures of size distribution within a fish population.

The second recent development in basic theory appears almost incidentally in a manuscript by Walters[1] documenting application software for the models of Deriso (1980) and Schnute (1985). Walters modified the assumption of knife-edged selectivity by assuming that *size*, rather than age, determines the cut-off for selection by the fishery. Although size

[1]C. J. Walters. 1986. Microcomputer stock assessment using Schnute's generalization of the Deriso delay-difference mode. User's manual for the computer program "SCHNUTE". Unpubl. ms. 43 p.

selection is an old concept in fisheries literature (e.g. Beverton and Holt 1957, p. 341ff.), Walters appears to be the first to have proposed its application to contemporary models based on difference equations. In his model, fish reach a critical size at various ages; consequently, the present state of the population depends on several past states. Mathematically, this feature allows the model to include a general autoregressive component and brings it closer the modern theory of times series analysis (Box and Jenkins 1970).

Walters presented his difference equation without proof, although his result is intuitively clear from earlier work by Deriso (1980) and Schnute (1985). Changing a major assumption, however, produces a new theory. In this paper, I show that if such a theory is developed systematically, it leads to a remarkably simple and comprehensive model similar to that proposed by Fournier and Doonan (1987). In particular, difference equations for arbitrarily high-order moments of the size distribution can be derived easily. Furthermore, the theory suggests a generalization of cohort analysis that includes size-dependent mortality. Taken together, the results derived here provide a global perspective of single-species fishery models.

Here is a brief outline of the paper. In Section 1, I formulate the main assumptions, which I apply in Section 2 to derive the principal difference equations. In Section 3, I describe how to tailor the model to a specific fishery, where model complexity relates to the data available. Finally, in Section 4, I derive a generalization of cohort analysis from the model hypotheses and show precisely how the difference equations of Deriso (1980) and Schnute (1985) fit into this context. The assumption that mortality is not size selective turns out to be a necessary requirement only for the last two groups of a multigroup model. Throughout the paper, I stress the biological significance of the results, so that the theory can be applied both conceptually and analytically.

The essential feature of the model here is that it is based on size, rather than age. To make this distinction clear, many of the results here are compared with earlier ones for age-structured models. Since the difference equations turn out to be particularly simple, one can assess intuitively their potential for parameter estimation. For example, high-order moments turn out to be informative only for parameters associated with fish growth. Also, the distribution of fish weights can be a useful indicator of natural mortality. Some surprising conclusions emerge from these analyses. For example, I show that the simple model of Deriso (1980) and Schnute (1985) can be deceptively wrong under certain circumstances and that an even simpler one should be used instead.

1. Model Assumptions

In this section, I develop a size-structured model by starting from assumptions familiar in age-structured models and replacing the age a with a suitable measure of fish size. For simplicity, I assume that size refers to weight, although other measures of size (such as length) can be used. The approach taken here might be shortened somewhat by dropping the analogy with age-structured models, but important comparisons between the two types of models would then have to be omitted. Of necessity, the development here involves considerable mathematical notation. The reader may wish to refer frequently to Appendix A, which lists definitions for all notation in the paper.

1A. Growth

The usual growth assumption in an age-structured model (e.g. Schnute 1985) is that the weight w_a at age a follows a von Bertalanffy growth curve:

$$w_a = W_\infty\left[1 - e^{-K(a-a_0)}\right] \tag{1.1}$$

where W_∞, K, and a_0 are three parameters that specify the curve. A short calculation (Ricker 1975, p. 222) from (1.1) shows that

$$w_{a+1} = W_\infty(1 - e^{-K}) + e^{-K}w_a. \tag{1.2}$$

This is a two-parameter relationship between a weight w_a and the succeeding weight w_{a+1} one year later. To obtain the growth model for a weight-structured population from (1.2), replace w_a by w and w_{a+1} by w′. Then (1.2) can be written

$$w' = W + \rho w \tag{1.3}$$

where

$$W = W_\infty(1 - e^{-K}) \tag{1.4a}$$

$$\rho = e^{-K}. \tag{1.4b}$$

Although they are both based on von Bertalanffy growth, equations (1.1) and (1.3) have rather different interpretations. In (1.1) the weight w_a at age a is a three-parameter function of the age a. Equation (1.3) does not assume that there is a definite relationship between age and weight. It asserts only that a fish starting at weight w will grow to weight w' within one year. The relationship is linear, having two parameters W and ρ. If there is an underlying age−weight relationship (1.1), then (1.4) can be used to estimate W and ρ from the von Bertalanffy parameters W_∞ and K.

A complete description of the growth model requires one constraint. Deriso (1980) and Schnute (1985) restrict (1.1) to ages above the recruitment age k:

$$a \geq k. \tag{1.5}$$

In this paper, I assume that (1.3) applies to weights above a specified recruitment weight V:

$$w \geq V. \tag{1.6}$$

Thus, (1.3) and (1.6) define a complete growth model in the sense that, for any weight w above the recruitment weight V, (1.3) specifies the succeeding weight w' one year later. The concept is that a fish may reach the weight V at several possible ages; however, once the weight V is reached, the growth curve (1.3) applies. This model contrasts with (1.1) and (1.5) in which the weight at each age conforms to (1.1) after age k.

The essential distinction between the two types of growth models can be summarized symbolically as follows:

Age-structured model: $a \rightarrow w$
Weight-structured model: $w \rightarrow w'$.

In the first case, the weight w is assumed to be a function of the age a. In the second, the weight w' after one year is a function of the starting weight w. Throughout this paper, the prime is used to denote such a function; that is, if u is a weight, then u' is the weight one year later. Furthermore, the tilde symbol is used to denote the inverse of this function; that is, $\tilde{u}$ denotes the starting weight which will result in weight u one year later:

$$(\tilde{u})' = u. \tag{1.7}$$

For example, the growth law (1.3) has the inverse

$$\tilde{w} = (w - W)/\rho. \tag{1.8}$$

This particular law is linear, and the linearity makes possible some of the results obtained here. However, other results are valid for any growth law ($w \to w'$). The main requirement for a *growth* law is that weights should increase, that is:

$$w' > w \tag{1.9}$$

for any weight $w \geq V$. In (1.3) this is equivalent to the requirement that $\rho > 0$.

A fish starting at weight V will (if it survives) reach weight V' in one year, weight $(V')'$ in two years, and so on. This suggests defining a sequence of weights V_i recursively as follows:

$$V_0 = V \tag{1.10a}$$

$$V_i = (V_{i-1})'. \tag{1.10b}$$

By (1.9), this sequence is increasing and so has a limit V_∞, which may be either finite or infinite. For example, for the growth law (1.3) it turns out that

$$V_i = \frac{1 - \rho^i}{1 - \rho} W + \rho^i V \tag{1.11}$$

where $(1 - \rho^i)/(1 - \rho)$ reduces to i when $\rho = 1$.Thus, if $\rho \geq 1$, then $V_\infty = \infty$; otherwise, $V_\infty = W/(1 - \rho)$.

The weights V_i in (1.10) can be used to define a series of half-open intervals as follows:

$$[V_0, V_1), [V_1, V_2), \ldots, [V_{i-1}, V_i), \ldots$$

where the notation $[V_0, V_1)$, for example, denotes the interval that includes V_0 and excludes V_1. We can think of the recruited population divided into groups, where the ith group consists of fish having weights in the ith interval. Surviving fish in group i move into group $i + 1$ one year later. In the year of recruitment, fish belong to the first group; that is, they have weights in the interval $[V, V')$. (Notice that a newly recruited fish must have weight less than V'; otherwise, its weight last year would have been at least the recruitment weight V.) The entire recruited population consists of fish with weights in the interval $[V, V_\infty)$.

The theory here is flexible in terms of the number of groups contemplated within the population. Most of this paper is devoted to a two-group model based on new recruits with weights in the interval $[V, V')$ and previously exploited fish with weights in $[V', V_\infty)$. It turns out that the models proposed by Deriso (1980) and Schnute (1985) involve only these two groups. In the paper's final section, I show that generalized cohort models, comparable with those of Fournier and Archibald (1982) and Deriso et al. (1985), can be obtained by extending the number of groups beyond these two.

1B. Population Variables

An age-structured model (e.g. Schnute 1985) involves the fundamental quantity N_{at}, the number of fish having age a at the start of year t. A basic difference between age and weight is that age is a discrete variable with integer values, while weight is continuous with real values. Consequently, to obtain a weight-structured model, one must replace the fundamental quantity N_{at} by a *density* $N(w, t)$. For this density, the integral

$$\int_{w_1}^{w_2} N(w,t)\,dw$$

represents the number of fish at the start of year t that have weight somewhere between w_1 and w_2. Thus, if w is measured in kg, then $N(w, t)$ has units kg^{-1}. Similarly,

$$\int_{w_1}^{w_2} wN(w,t)\,dw$$

represents the weight (biomass) of fish at the start of year t that have weight between w_1 and w_2.

Following Schnute (1985), let N_t and N_t^* represent the number and biomass, respectively, of recruited fish in the fishery at the start of year t. Then, by definition, it follows that

$$N_t = \int_V^{V_\infty} N(w,t)\,dw \tag{1.12}$$

$$N_t^* = \int_V^{V_\infty} wN(w,t)\,dw. \tag{1.13}$$

As described earlier, the recruited population N_t has two components: newly recruited fish with weights in $[V, V')$ and previously exploited fish with weights in $[V', V_\infty)$. Let R_t and P_t denote the number of fish in each component, respectively, at the start of year t, and let R_t^* and P_t^* represent the corresponding biomasses. Then, by definition,

$$R_t = \int_V^{V'} N(w,t)\,dw \tag{1.14}$$

$$R_t^* = \int_V^{V'} wN(w,t)\,dw \tag{1.15}$$

$$P_t = \int_{V'}^{V_\infty} N(w,t)\,dw \tag{1.16}$$

$$P_t^* = \int_{V'}^{V_\infty} wN(w,t)\,dw. \tag{1.17}$$

Mathematically, definitions (1.12)–(1.17) correspond to moments of the density $N(w, t)$. This feature plays an important role in the derivation and interpretation of difference equations given later.

A sensitive reader might have concerns about definitions (1.14)–(1.15) for the newly recruited population, since a fish smaller than weight V at the start of year t could grow into the interval $[V, V')$ during the year. Because t is restricted to integer values corresponding to individual years, the model here implicitly assumes that growth occurs instantly at the end of each year. During the year, the population's size structure remains stable, since mortality (fishing and natural) is assumed not be size selective for weights above V. In practice, the recruitment weight V should be chosen with this approximation in mind.

1C. Population Dynamics

An age-structured model always contains one fundamental dynamic equation that describes the process of aging one year. For example, the first assumption in Schnute's (1985) model is

$$N_{a+1,\,t+1} = \tau_t N_{at} \tag{1.18}$$

where τ_t is the total survival from fishing and natural mortality during year t. The key feature of this assumption is that survival is independent of age a for $a \geq k$. Biologically, this feature corresponds to knife-edged selectivity; analytically, it makes possible the derivation of a difference equation in the total population N_t.

The counterpart of (1.18) for a weight-structured population

is based on two principles. First, in analogy with age-independent survival, the total survival τ_t is presumed independent of weight w for $w \geq V$. Second, just as a fish of age a must move to age $a + 1$ in one year, so also a fish of weight w must grow in one year to weight w'. These principles imply that

$$(1.19) \qquad \int_{w_1'}^{w_2'} N(w, t+1)dw = \tau_t \int_{w_1}^{w_2} N(w,t)dw$$

for every weight interval $[w_1, w_2]$ with $V \leq w_1 < w_2$. This is the fundamental dynamic equation for a weight-structured model. It states that fish in an arbitrary weight interval $[w_1, w_2]$ must, after survival during one year, reach the weight interval $[w_1', w_2']$.

Mathematically, (1.19) is written in integral form. To obtain an equivalent differential form, notice that if w_2 is close to w_1, then (1.19) implies the approximate equation

$$N(w_1', t+1)(w_2' - w_1') \cong \tau_t N(w_1, t)(w_2 - w_1).$$

Taking the limit as w_2 moves to w_1 gives the exact result

$$(1.20) \qquad N(w', t+1)\frac{dw'}{dw} = \tau_t N(w,t)$$

for every $w \geq V$, where the subscript on w_1 has been dropped. Incidentally, the derivative dw'/dw in (1.20) is the Jacobian of the transformation from w to w'.

Equations (1.19) and (1.20) are equivalent forms of the same dynamic assumption for a weight-structured populations. They are valid for *any* growth law, $w \rightarrow w'$. Furthermore, they can easily be extended to cover the case where mortality is size-selective by assuming that τ_t is a function of size, $\tau_t(w)$. This would require placing τ_t inside the integral on the right side of (1.19), but (1.20) remains valid even when τ_t is replaced by $\tau_t(w)$. I return to this point in Section 4, where I derive generalized cohort analysis; however, in the meantime, I restrict my attention to knife-edged selectivity, for which τ_t is independent of w.

1D. Average Weights

Average weights play an important role in size-structured models. For example, let X_t be the average weight of the entire recruited population at the start of year t; that is,

$$(1.21) \qquad X_t = N_t^*/N_t.$$

Because mortality is presumed not be be size selective for weights above V, this average will not change during the year; thus, X_t also represents the average weight *throughout* year t. Another consequence of knife-edge selectivity is that the weight distribution of the catch follows that of the population; thus, X_t can be estimated directly from a sample of the catch. Incidentally, this discussion shows that it is important to make a judicious choice of the recruitment weight V. In some cases, it may be wise to pick a rather large V and to exclude from the catch fish smaller than V, treating them as part of the natural mortality that precedes recruitment.

In analogy with (1.21), let Y_t and Z_t denote average weights within the newly recruited and previously exploited components of the population, respectively; that is,

$$(1.22) \qquad Y_t = R_t^*/R_t$$

$$(1.23) \qquad Z_t = P_t^*/P_t.$$

Like X_t, these remain fixed during year t, and they can be estimated from a sample of the catch. For example, Z_t is the average weight in year t of fish with weight greater than V'.

In age-structured models such as those of Deriso (1980) and Schnute (1985), newly recuited fish all have the same weight V, so that

$$(1.24a) \qquad Y_t = V.$$

A more reasonable value of Y_t in a size-structured population might be

$$(1.24b) \qquad Y_t = (V + V')/2$$

based on the assumption that new recruits have weights distributed evenly across the interval $[V, V')$. In general, Y_t can be any value between V and V', depending on the underlying weight distribution. This illustrates one of the differences between age- and size-structured models.

A significant feature of (1.24a)–(1.24b) is that Y_t is *independent of* t. In general, this is true if the new recruits are distributed similarly each year, that is, if there is a function $f(w)$ independent of t such that

$$(1.25) \qquad N(w,t) = f(w)N(V,t); \quad V \leq w < V'$$

for every year t. If (1.25) holds for the entire range $V \leq w < V_\infty$, then the averages X_t and Z_t are also independent of t. Stable fish populations typically experience only minor fluctuations in average weights X_t, Y_t, and Z_t. The proofs below suggest that such populations may need to be modeled differently from those in which X_t experiences large variation.

1E. Recruitment

The most fundamental difference between age- and weight-structured models pertains to recruitment. As described in the introduction, the age-structured models of Deriso (1980) and Schnute (1985) involve a specific time lag k, the recruitment age, between birth and recruitment. In a size-structured model, the time lag between birth and a fixed recruitment weight V can be variable, depending on how many years it takes a fish to reach the critical size. To be precise, suppose that k and K are the minimum and maximum age, respectively, at which a fish can reach a weight in the interval $[V, V')$. Let S_t^* be the spawning stock biomass in year t and assume that some function $F(S_t^*)$ can be used to calculate the total recruitment biomass in future years $(t + k, \ldots, t + K)$ due to the stock biomass in year t. Assume further that the fraction π_a of this total recruitment is recruited at age a $(a = k, \ldots, K)$. Notice that the function $F(\cdot)$ and the fraction π_a are presumed independent of t, although these simplifying restrictions can easily be generalized. The above assumptions imply Walters' recruitment hypothesis for a weight-structured population (see footnote 1):

$$(1.26) \qquad R_t^* = \sum_{a=k}^{K} \pi_a F(S_{t-a}^*).$$

The parameters π_a $(a = k, \ldots, K)$ are, of course, subject to the restrictions that they are fractions summing to 1:

$$(1.27a) \qquad 0 < \pi_a \leq 1$$

$$(1.27b) \qquad \sum_{a=k}^{K} \pi_a = 1.$$

In the special case that $k = K$, a weight-structured model reduces essentially to an age-structured one.

The assumption (1.26) differs slightly from a comparable assumption in Schnute (1985) where the number of recruits R_t, rather than the biomass R_t^*, is presumed dependent on an earlier stock size. Either choice, R_t or R_t^*, in (1.26) gives similar results, but slightly greater symmetry is achieved by choosing R_t^*. Another alternative to (1.26) might be

$$(1.28) \quad R_t^* = \sum_{a=k}^{K} \pi_a \sigma^{a-k} F(S_{t-a}^*)$$

where σ is a survival fraction. In (1.26), $F(S^*)$ represents the total biomass recruited to the fishery over a period of $K - k + 1$ yr. In (1.28), $F(S^*)$ is the biomass at age k destined to be recruited at an age between k and K. Natural mortality reduces this biomass by the fraction σ each year prior to actual recruitment. The two formulations (1.26) and (1.28) can be shown to give equivalent results, after suitably altering the definitions of various parameters. Although (1.28) is closer to the usual definition of recruitment in the context of cohort analysis, I use the simpler form (1.26) here.

Numerous forms for the recruitment functions $F(S^*)$ have been proposed in the literature, and in an earlier paper (Schnute 1985, equations (1.30)–(1.36), I suggested using

$$(1.29) \quad F(S^*) = \alpha S^* (1 - \beta\gamma S^*)^{1/\gamma},$$

a function that includes most historical alternatives, such as those of Ricker (1954, 1958), Schaefer (1954, 1957), Beverton and Holt (1957), and Pella and Tomlinson (1969). Unfortunately, all these models have the property that $F(0) = 0$; consequently, they do not extend continuously to the case of constant recruitment. Practical experience (Jacobson et al. 1987) shows that this can be a serious limitation. It is true, of course, that recruitment must be 0 when the stock is 0; however a curve through the available range of data need not extrapolate to the origin. This is precisely the traditional argument used in conjunction with von Bertalanffy growth (1.1): a useful growth model need not predict that a fish starts growing at age 0 with size 0. An extension of (1.29) along the lines of (1.1) is

$$(1.30) \quad F(S^*) = \alpha(S^* - \delta)[1 - \beta\gamma(S^* - \delta)]^{1/\gamma}$$

where δ is the extrapolated stock biomass at which $F = 0$, just as a_0 in (1.1) is the extrapolated age at size 0.

This modification of (1.29) preserves its desirable global properties. For example, by a proof similar to that in Schnute (1985, appendix B), (1.30) can be shown to be equivalent to

$$(1.31) \quad F(S^*) = G\frac{S^* - \delta}{H - \delta}\left[1 + \gamma\frac{H - S^*}{H - \delta}\right]^{(1/\gamma)}$$

where G and H are two parameters defined by

$$(1.32a) \quad G = \alpha\beta^{-1}(1 + \gamma)^{-(1+\gamma)/\gamma}$$

$$(1.32b) \quad H = \delta + [\beta(1 + \gamma)]^{-1}.$$

When $\gamma > -1$ in (1.31), $F(S^*)$ takes the maximum value G at $S^* = H$, and when $\gamma = 1$, (1.31) reduces to the constant recruitment function

$$(1.33) \quad F(S^*) = G.$$

Schnute (1985, fig. 3) illustrated the family of curves (1.31) when $\delta = 0$, and the possibility that $\delta \neq 0$ simply removes the restriction that the curves should pass through the origin by allowing translation to the right ($\delta > 0$) or left ($\delta < 0$). In many applications, $\delta < 0$ and $F(0) > 0$.

Each of the equivalent recruitment curves, (1.30) and (1.31), has four parameters. Typically, it is impossible to estimate so many parameters, and some restriction is required. For example, when $\delta = 0$, the choices $\gamma = -1$, 0, or 1 in (1.30) correspond to the Beverton–Holt, Ricker, or Schaefer curves, respectively (Schnute 1985, section 1E). The curves described here are designed to accommodate both the historical alternatives and the practical limitations of real data sets.

1F. Summary

I have discussed the development of a weight-structured model in relation to more familiar age-structured assumptions. There are only three key assumptions in the new model. First, there is the growth equation (1.3), together with the concept of a more general growth law ($w \to w'$). Second, there is the dynamic equation (1.19), which is restated in differential form in (1.20). Finally, there is the recruitment hypothesis (1.26), which includes several time lags in the recruitment calculation. Although these three principles require some elaboration to become practically useful, they are adequate for deriving an interesting and useful general theory.

2. Difference Equations

A modified version of Schnute's (1985) methods can be used to derive difference equations similar to those of Deriso (1980) and Schnute (1985), based on the model hypotheses formulated above. A deeper perspective is possible, however, by generalizing the moment definitions (1.12)–(1.17) and applying a single method to obtain a complete set of moment equations. This approach parallels that of Fournier and Doonan (1987), although it leads in the present context to simpler results that can easily be interpreted biologically.

The essential distinction between the model here and that of Fournier and Doonan (1987) is the underlying structure variable. They used age, and I use size. To handle the problem of gear selectivity, they assumed that fish of a single age may belong to several groups with distinct vulnerabilities to the gear. I handle the problem differently, by assuming that selectivity relates directly to size; that is, that fish in a single weight interval are all equally vulnerable. Thus, they divided one age group into subgroups of differing vulnerability, while I do not similarly divide the fish within one size group. Since one of my size groups can include fish of several ages, these two analyses have something in common. My analysis is more rigid than theirs, however, because I apply my growth law (1.3) deterministically, while they assumed only that *mean* sizes at age follow a growth curve like (1.1). In my view, the model here is a compromise in favor of simplicity, although the greater complexity of their model may sometimes be required. Incidentally, the full significance of my selectivity hypothesis does not become clear until Section 4, where I derive generalized cohort analysis.

2A. Higher Order Moments

Notation presented so far has focussed on familiar population variables, such as numbers and biomass. As discussed above in connection with (1.12)–(1.17), these variables are moments of the underlying density $N(w, t)$. More generally, define nth-order moments as follows:

$$(2.1) \quad N_t^{[n]} = \int_V^{V_\infty} w^n N(w, t)dw$$

$$(2.2) \qquad R_t^{[n]} = \int_V^{V'} w^n N(w,t)dw$$

$$(2.3) \qquad P_t^{[n]} = \int_{V'}^{V_\infty} w^n N(w,t)dw.$$

For $n = 0$ or 1, these are the usual measures of numbers and biomass, respectively. For example, $N_t^{[0]} = N_t$ and $N_t^{[1]} = N_t^*$; thus, the superscript "[0]" on N_t can be dropped and "[1]" can be replaced with "*". The quantities (2.1)–(2.3) represent population *moments about the origin* (Kendall and Stuart 1977, p. 57). Similarly, define *central moments about the mean* as follows:

$$(2.4) \qquad N_t^{(n)} = \int_V^{V_\infty} (w - X_t)^n N(w,t)dw$$

$$(2.5) \qquad R_t^{(n)} = \int_V^{V'} (w - Y_t)^n N(w,t)dw$$

$$(2.6) \qquad P_t^{(n)} = \int_{V'}^{V_\infty} (w - Z_t)^n N(w,t)dw.$$

For $n = 0$, the central moments (2.4)–(2.6) are the same as (2.1)–(2.3), respectively. For $n = 1$, these moments are 0, as can be verified from the definitions (1.21)–(1.23) of X_t, Y_t, and Z_t. For $n \geq 2$, the moments (2.4)–(2.6) measure the dispersion of weights within the population. The average values,

$$(2.7) \qquad X_t^{(n)} = N_t^{(n)} / N_t$$

$$(2.8) \qquad Y_t^{(n)} = R_t^{(n)} / R_t$$

$$(2.9) \qquad Z_t^{(n)} = P_t^{(n)} / P_t,$$

have straightforward biological interpretations. For example, $X_t^{(2)}$ is the weight variance in year t among fish with weight $w \geq V$, and $Z_t^{(2)}$ is the variance among fish with weight $w \geq V'$.

The average dispersions (2.7)–(2.9) all have units kg^n when weight is measured in kg. They can be estimated directly from a random sample of the catch. (Again, knife-edge selectivity above weight V implies that the catch has the same weight structure as the recruited population.) To be precise, suppose that a sample of M fish in year t includes the weights w_1, w_2, w_M. Then the sample mean $\bar{w}$ provides an estimate for X_t, and an estimate for $X_t^{(n)}$ is

$$(2.10a) \qquad \hat{X}_t^{(n)} = \frac{1}{M} \sum_{i=1}^{M} (w_i - \bar{w})^n.$$

Similar estimates for $Y_t^{(n)}$ and $X_t^{(n)}$ are obtained by restricting the sample to fish with weights in the intervals $[V, V')$ and $[V', V_\infty)$, respectively. For example, suppose that M_z (with $M_z \leq M$) fish in the sample have weights at least V'. Denote these weights by z_i ($i = 1, \ldots, M_z$), where $z_i \geq V'$. Then the subsample mean $\bar{z}$ gives an estimate for Z_t, and an estimate for $Z_t^{(n)}$ is

$$(2.10b) \qquad \hat{Z}_t^{(n)} = \frac{1}{M_z} \sum_{i=1}^{M_z} (z_i - \bar{z})^n.$$

It is important to notice that the means and sample sizes in (2.10a) and (2.10b) are different. Incidentally, estimates like (2.10a) and (2.10b) can be corrected for small sample bias, but a serious approach to this problem would involve the definitions of k-statistics and cumulants (Kendall and Stuart 1977, chap. 12 and 13). Such elaborate procedures are unnecessary here, given that reasonable sample sizes M are possible and that other sources of error typically dominate the sample bias in (2.10a) and (2.10b).

2B. First Version of the Moment Equation

It is remarkably easy to derive a general dynamic equation for nth-order population moments, based on the model developed in Section 1. The key idea is to multiply the dynamic equation (1.20) by w'^n and then to integrate w from V to V_∞. This gives

$$(2.11) \qquad \int_V^{V_\infty} w'^n N(w', t+1) \frac{dw'}{dw} dw = \tau_t \int_{V'}^{V_\infty} w'^n N(w', t)dw.$$

In the left side of (2.11), the expression $(dw'/dw)dw$ reduces to dw', and the integration variable can be converted from w to w'. The range of integration then goes from V' to V_∞, since ${V_\infty}' = V_\infty$. Thus:

$$(2.12a) \qquad \int_V^{V_\infty} w'^n N(w', t+1) \frac{dw'}{dw} dw = \int_{V'}^{V_\infty} w'^n N(w', t+1)dw'$$

$$(2.12b) \qquad = P_{t+1}^{[n]}$$

where (2.12b) follows from the definition (2.3). The right side of (2.11) can be simplified using the fact that $w' = W + \rho w$; thus, by the binomial theorem:

$$(2.13) \qquad w'^n = \sum_{i=0}^{n} \binom{n}{i} W^{n-i} \rho^i w^i$$

where $\binom{n}{i}$ denotes the usual binomial coefficient. Thus, the right side of (2.11) reduces essentially to a sum of integrals involving powers of w times $N(w,t)$, that is, moments of N about the origin. Combining (2.11)–(2.13) gives

$$(2.14) \qquad P_{t+1}^{[n]} = \tau_t \sum_{i=0}^{n} \binom{n}{i} W^{n-i} \rho^i N_t^{[i]}.$$

I refer to (2.14) as the first version of the general moment equation of order n. A second version, which involves central population moments, is presented later.

Notice that (2.14) involves the population moments (2.1) and (2.3), the survival fraction τ_t, and the parameters W and ρ from the growth law. This result is based on only two assumptions, the dynamic law (1.20) and the growth law (1.3). Furthermore, (2.14) is easy to prove. Multiplying (1.20) by w'^n and integrating the result gives (2.11). This equation simplifies by changing the variable of integration from w to w' on the left and by applying the binomial theorem to w'^n on the right.

The expansion (2.13) demonstrates why binomial coefficients appear in the general moment equation, as first discovered by Fournier and Doonan (1987, equation (10.2) and theorems 2 and 4). In particular, these coefficients occur because of the linear growth law (1.3). They can, however, be eliminated from the analysis by reformulating (2.14) in terms of central moments. I explain this simplification in deriving the second version of the moment equation later.

From a biological point of view, (2.14) describes the transition of the entire recruited population in year t to the previously exploited population in year $t + 1$. Thus, moments $N_t^{[i]}$ ($i =$

$0, \ldots, n$) on the right side of (2.14) are used to compute $P_{t+1}^{[i]}$ on the left. Two processes, survival and growth, are involved in this transition. The factor τ_t accounts for survival, and the binomial expansion accounts for growth.

2C. Equations of Orders 0 and 1

To relate (2.14) to earlier work by Deriso (1980) and Schnute (1985), notice from definitions (2.1)–(2.3) that

$$P_t^{[n]} = N_t^{[n]} - R_t^{[n]} \tag{2.15}$$

for each n and t. In particular, by combining (2.14) and (2.15) when $n = 0$, we obtain the moment equation of order 0:

$$N_{t+1} - R_{t+1} = \tau_t N_t. \tag{2.16}$$

This has the obvious interpretation that the population in year $t + 1$, except for recruits, consists of survivals from the previous year t. Similarly, when $n = 1$, (2.14) reduces to

$$N_{t+1}^* - R_{t+1}^* = \tau_t (\rho N_t^* + W N_t), \tag{2.17}$$

the moment equation of order 1.

As it stands, the biological interpretation of (2.17) is not entirely clear. To obtain a more meaningful version, rewrite (2.17) in the form

$$N_{t+1}^* - R_{t+1}^* = \tau_t \left(\rho + \frac{W}{X_t}\right) N_t^*$$

using definition (1.21) for the average weight X_t of the recruited population. The growth law (1.3) implies that

$$\rho + \frac{W}{X_t} = \frac{W + \rho X_t}{X_t} = \frac{X_t'}{X_t},$$

and thus, (2.17) is equivalent to

$$N_{t+1}^* - R_{t+1}^* = \tau_t (X_t'/X_t) N_t^*. \tag{2.18}$$

This version of (2.17) has an interpretation analogous to that for (2.16). It states that the biomass in year $t + 1$, except for recruitment, consists of the biomass surviving from the previous year t, adjusted for growth by the factor X_t'/X_t. This adjustment factor is the key detail. It implies that biomass growth depends only on *average* weights; thus, the average weight X_t projects forward to an average weight X_t' determined by the growth law (1.3). I discuss this point further in developing the second version of the moment equation below.

Remarkably, fisheries literature has previously ignored (2.18). It is a simple first-order difference equation with a clear interpretation. Furthermore, if the average weight X_t were known for each year t, (2.18) could be used as the basis of a practical model similar to models proposed by Deriso (1980) or Schnute (1985). Their models, however, are based on *second*-order difference equations.

To understand the distinction between (2.18) and earlier models, notice that (2.16)–(2.17) involve both the biomass N^* and the population N at various times. These equations can be combined to give a single equation in biomasses alone. To achieve this, write a second version of (2.17) at time $t - 1$, multiply it by τ_t, and subtract the result from (2.17). This calculation gives

$$\begin{aligned} N_{t+1}^* - R_{t+1}^* - \tau_t (N_t^* - R_t^*) \\ = \rho\tau_t (N_t^* - \tau_{t-1} N_{t-1}^*) + W\tau_t (N_t - \tau_{t-1} N_{t-1}). \end{aligned} \tag{2.19}$$

From (2.16) at time $t - 1$, the expression $N_t - \tau_{t-1} N_{t-1}$ on the right side of (2.19) reduces to R_t. Furthermore, from (1.22):

$$R_t = R_t^* / Y_t$$

so that (2.19) is equivalent to

$$\begin{aligned} N_{t+1}^* - \tau_t N_t^* - R_{t+1}^* \\ = \rho\tau_t \left[N_t^* - \tau_{t-1} N_{t-1}^* + \frac{1}{\rho}\left(\frac{W}{Y_t} - 1\right) R_t^*\right]. \end{aligned} \tag{2.20}$$

The right side of (2.20) can be simplified using the calculation

$$\frac{1}{\rho}\left(\frac{W}{Y_t} - 1\right) = \rho^{-1} (W - Y_t)/Y_t = -\tilde{Y}_t/Y_t$$

where $\tilde{Y}_t$ is defined by (1.7)–(1.8). Consequently,

$$\begin{aligned} N_{t+1}^* - \tau_t N_t^* - R_{t+1}^* \\ = \rho\tau_t [N_t^* - \tau_{t-1} N_{t-1}^* - (\tilde{Y}_t/Y_t) R_t^*]. \end{aligned} \tag{2.21}$$

This result is identical to equation (2.4) in Schnute (1985, p. 420) in the special case (1.24a) that $Y_t = V$; the symbol v in that paper has the same meaning as $\tilde{V}$ here. Indeed, the general size-structured model includes an age-structured one as a special case, by assuming that fish at each age have a fixed weight determined by the growth curve. Thus, the proof leading to (2.21) constitutes an alternative proof of the fundamental difference equations in Deriso (1980) and Schnute (1985).

The distinction between (2.18) and the Deriso–Schnute model (2.21) is now clear. The first-order moment equation (2.17) involves not only the biomass N_t^* but also the population N_t. There are two ways to eliminate N_t: either use a knowledge of the average weight X_t to obtain (2.18) or use both (2.16)–(2.17) to obtain (2.21). In brief, the modeler seems to be faced with two alternatives: either use the first-order difference equation (2.18) plus extra data or resort to the second-order difference equation (2.16). As I show later, there are better choices than either of these, but I include the next section to demonstrate that the Deriso–Schnute model (2.21) can be deceptive and should be used with extreme caution.

2D. Constant Average Weight

In an earlier work (Schnute 1985), I have stressed that the difference equations define a *class* of models for iterative model construction, as described by Box and Jenkins (1970). Thus, biologically meaningful special cases have considerable significance to the modeler. Unfortunately, the numerous cases outlined in Schnute (1985) omit an interesting possibility based on the new equation (2.18). To put this possibility into perspective, consider first the very simple case in which all fish have the same weight. This occurs if $W = 0$ and $\rho = 1$ in (1.3), since then $w' = w$ (i.e. the weight is constant). Making these choices for W and ρ in (2.17) gives

$$N_{t+1}^* - R_{t+1}^* = \tau_t N_t^*, \tag{2.22}$$

the biomass equation for a population with constant weight. This rather obvious result can also be obtained by multiplying both sides of (2.16) by the weight of a fish, presumed constant. In addition, (2.22) follows from (2.18) by noting that $X_t' = X_t$ in this case.

A much less restrictive assumption than constant weight for all fish is that only the *average* weight X_t of the recruited population is independent of the year t; that is,

(2.23) $X_t = X$

for all t. Then it follows from (2.18) that

(2.24) $N^*_{t+1} - R^*_{t+1} = \tau_t (X'/X) N^*_t$.

The three biomass equations (2.22), (2.24), and (2.21) form a hierarchy of ascending complexity. The simplest possibility (2.22), cited earlier by Schnute (1985, model G3 in table 3), assumes that all fish in the population have the same weight. Equation (2.24) is only slightly more complicated than (2.22), yet it allows a full distribution of fish weights and assumes only that averages weights X_t are constant. The final possibility (2.21) involves no restrictive assumptions other than those that define the general model.

A simple analogy illustrates the problem with using the complex model (2.21) when (2.24) is adequate. Suppose that a time series x_t is generated by a noisy process in which the deterministic part is

(2.25) $x_{t+1} = bx_t$.

It follows from (2.25) that for *any* value of c:

(2.26) $x_{t+1} - bx_t = c(x_t - bx_{t-1})$.

If, however, we try to use the series x_t to estimate c in (2.26), two outcomes are inevitable: first, the estimate for c will be nonsense because the data have been generated independent of c, and second, the estimate for b will be prejudiced in some way. (For example, the loss of a degree of freedom for c will widen the confidence interval for b.) It turns out that if (2.24) applies, then the derivation of (2.21) is similar to the derivation of (2.26) from (2.25). This simple artifact may underlie many practical difficulties encountered in the use of models proposed by Deriso (1980) and Schnute (1985).

2E. Second Version of the Moment Equation

The principal result derived so far is the general moment equation (2.14), which follows from the dynamic equation (1.20) by the proof outlined in (2.11)–(2.13). Furthermore, when n is 0 or 1, (2.14) takes the form (2.16) or (2.18), respectively. These two special cases have particularly clear biological meaning: (2.16) describes the dynamics of population numbers, and (2.18) similarly describes biomass dynamics with the extra dimensionless factor X'_t/X_t to adjust for growth. It is reasonable to ask whether or not a counterpart of (2.18) exists for the general moment equation (2.14). In other words, is there an equation that expresses the dynamics of nth-order moments (with $n \geq 2$) in terms of survival and a dimensionless growth factor? The answer is yes, as long as we reformulate the problem in terms of the central moments (2.4) and (2.6).

The derivation begins with a simple conclusion from (2.16) and (2.18). Divide the latter by the former to obtain

(2.27) $$\frac{P^*_{t+1}}{P_{t+1}} = \frac{X'_t}{X_t} \cdot \frac{N^*_t}{N_t},$$

a result based on the fact that the left sides of (2.16) and (2.18) are P_{t+1} and P^*_{t+1}, respectively. By (1.23), the left side of (2.27) is Z_{t+1}, and by (1.21), the right side is $(X'_t/X_t)X_t$, which reduces to X'_t. Thus, (2.27) implies that

(2.28) $Z_{t+1} = X'_t$.

This conclusion has the simple interpretation that the average weight of previously exploited fish in year $t + 1$ equals the average weight of the entire recruited population in year t *projected forward by the growth law*. Notice that the change in mean weights described by (2.28) is independent of mortality, a result consistent with the assumption that mortality is not selective for size.

TABLE 1. Two versions of the system of general moment equations. The system ⟨A⟩ for $n \geq 0$ is equivalent to ⟨B0⟩, ⟨B1⟩, and ⟨B2⟩ for $n \geq 2$. The first system involves moments about the origin, while the second is based on central moments. Equation ⟨B0⟩ describes survival from year t to $t + 1$, and ⟨B1⟩ and ⟨B2⟩ relate to growth during year t. Specifically, ⟨B1⟩ and ⟨B2⟩ describe changes in mean and dispersion, respectively, of the underlying weight distribution. Figure 1 illustrates such changes for three values of ρ.

Label	Text No.	Equation
⟨A⟩	(2.14)	$P^{[n]}_{t+1} = \tau_t \sum_{i=0}^{n} \binom{n}{i} W^{n-i} \rho^i N^{[i]}_t$
⟨B0⟩	(2.16)	$P_{t+1} = \tau_t N_t$
⟨B1⟩	(2.28)	$Z_{t+1} = W + \rho X_t$
⟨B2⟩	(2.33)	$Z^{(n)}_{t+1} = \rho^n X^{(n)}_t$

The second version of the moment equation can be obtained by a proof similar to the first, with a modification that takes account of (2.28). The idea is to multiply the left side of the dynamic law (1.20) by $(w' - Z_{t+1})^n$ and the right side by $(w' - X'_t)^n$. By (2.28), both sides are thus multiplied by equal quantities. Integrating from V to V_∞ gives

(2.29) $$\int_V^{V_\infty} (w' - Z_{t+1})^n N(w', t+1) \frac{dw'}{dw} dw = \tau_t \int_V^{V_\infty} (w' - X'_t)^n N(w, t) dw,$$

a result comparable with (2.11). The left side of (2.29) simplifies by the process applied in (2.12); that is, the integration variable can be converted from w to w' and the integration range is then the interval $[V', V_\infty)$. With reference to the definition (2.6), this proves that

(2.30) $$\int_V^{V_\infty} (w' - Z_{t+1})^n N(w', t+1) \frac{dw'}{dw} dw = P^{(n)}_{t+1}.$$

To simplify the right side of (2.29), notice from the growth law (1.3) that

$$(w' - X'_t)^n = \rho^n (w - X_t)^n.$$

Consequently, with reference to the definition (2.4):

(2.31) $$\int_V^{V_\infty} (w' - X'_t)^n N(w, t) dw = \rho^n N^{(n)}_t.$$

Combining (2.29)–(2.31) gives the second version of the general moment equation:

(2.32) $P^{(n)}_{t+1} = \rho^n \tau_t N^{(n)}_t$.

Notice three key features of (2.32). First, it is a dynamic equation in central population moments. Second, it does not involve the binomial coefficients that appear in the first general moment equation (2.14); indeed, (2.32) is strikingly simpler than (2.14). Third, since central moments (for $n \geq 2$) measure dispersion, (2.32) has a simple biological interpretation. The dispersion of the previously exploited population in year $t + 1$

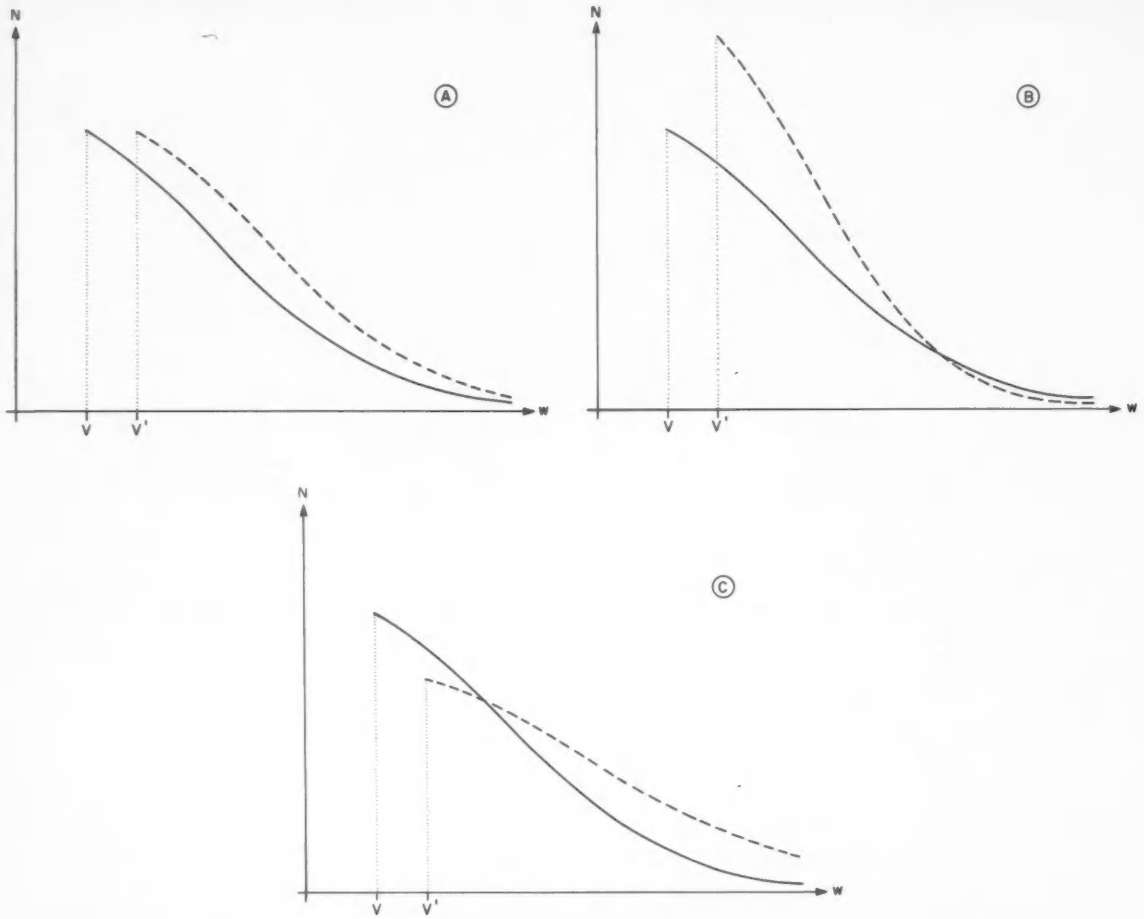

FIG. 1. Solid curve $N(w,t)$ with $w \geq V$, and broken curve $N(w,t+1)$ with $w \geq V'$. The transition from time t to $t+1$ is based on the dynamic law (1.19) or (1.20) with $\tau_t = 1$. (A) $\rho = 1$ and dispersion is unchanged; (B) $\rho < 1$ and dispersion is reduced; (C) $\rho > 1$ and dispersion is increased.

is a multiple of the dispersion of the recruited population in year t.

The moment equation (2.32) expresses a deep, yet simple consequence of the linear growth law (1.3). Divide (2.32) by (2.16) and use definitions (2.7) and (2.9) to show that

$$Z_{t+1}^{(n)} = \rho^n X_t^{(n)}. \tag{2.33}$$

As summarized in Table 1, this result is almost equivalent to the general moment equation. More precisely, the general equation ⟨A⟩ is equivalent to a set of dynamic equations: ⟨B0⟩ for population numbers, ⟨B1⟩ for mean weights, and ⟨B2⟩ for weight dispersions with $n \geq 2$. Figure 1 illustrates the significance of ⟨B1⟩ and ⟨B2⟩. In each panel, the solid curve represents $N(w,t)$ for $w \geq V$ and the broken curve represents $N(w,t+1)$ for $w \geq V'$ after 1 yr of growth. For simplicity, the panels all assume that $\tau_t = 1$, since nonselective mortality has no effect on weight moments, as discussed earlier. Figure 1A represents the case when $\rho = 1$. In this case, all fish grow by a fixed increment, and the broken curve is simply a translation of the solid one. Such a translation is consistent with the prediction from ⟨B2⟩ that the dispersion is identical for solid and broken curves when $\rho = 1$. In Fig. 1B, $\rho < 1$ so that small fish grow more rapidly than large fish. This causes the gap between small and large fish to be reduced. As a result, the broken curve is less dispersed than the solid one, just as ⟨B2⟩ predicts when $\rho < 1$. Similarly, Fig. 1C illustrates that when $\rho > 1$, large fish grow more rapidly than small fish. This increases the dispersion of weights within the population, as predicted by ⟨B2⟩ when $\rho > 1$. In all three panels, ⟨B1⟩ describes the shift to the right from solid to broken curves, corresponding to overall growth of the population.

The second version of the moment equation shows that moments of order 2 or higher relate to only one model parameter: ρ. Based on (2.33), a linear regression of $Z_{t+1}^{(n)}$ on $X_t^{(n)}$ constrained through the origin might give a slope estimate for ρ^n. However, in the framework of the model here, the modeler should not expect to improve estimates of other parameters by using moment equations with order $n \geq 2$. This means that the simple equation (2.18) is likely to play a dominant role in practical biomass models.

3. Model Development

The previous section describes how to obtain various difference equations for a size-structured population. To apply these equations in a specific case, the modeler requires further hypotheses related to the data available. In an earlier paper (Schnute 1985), I proposed one possible set of hypotheses in the context of catch and effort data for an age-structured population. To illustrate the flexibility of that model, I cited 24 cases of special interest. More recent experience suggests, however, that even this list is too narrow. Probably no single collection of additional hypotheses can ever prove adequate for all situations, and the modeler must always consider alternatives specific to the case under consideration. In this paper, the key assumptions used so far are the growth law (1.3) and the dynamic equation (1.19). The recruitment law (1.26) is also implicit in any difference equation involving the recruitment biomass R_t^* at some time t. Three aspects of the fishery remain to be included: the particulars of natural and fishing mortality, the process and timing of recruitment, and the means (such as catch per unit effort) whereby the population is indexed. In this section, I propose three further hypotheses and show how these can be used to develop a complete model for the available data.

3A. Model Details

The key mathematical object of the theory so far is a population density function $N(w,t)$. To develop a practical model, it is convenient to introduce three additional densities: $C(w,t)$ for the catch, $S(w,t)$ for the spawning stock, and $I(w,t)$ for the population index. These have interpretations similar to that for $N(w,t)$. For example,

$$\int_{w_1}^{w_2} C(w,t)\,dw$$

represents the number of fish caught during year t with weights between w_1 and w_2. The population index might be a quantity like catch per unit effort, in which case the integral

$$\int_{w_1}^{w_2} I(w,t)\,dw$$

would be the number of fish in the weight interval $[w_1, w_2]$ caught per unit of effort in year t. The quantities C_t, C_t^*, S_t, S_t^*, I_t, and I_t^* can all be defined by analogy with the definitions (1.12)–(1.13) for N_t and N_t^*. Thus, for example, S_t and S_t^* represent number and biomass, respectively, of fish that spawn in year t.

The quantities C, S, and I are associated with processes that take place in the fishery: catching fish, spawning, and indexing the population. These processes have one feature in common: their significance depends on timing. Is the catch removed before, during, or after natural mortality? How much mortality occurs before spawning? Does the index apply to the population at the start of the year, or after some mortality has occurred? I address the question of timing in each case by introducing a timing parameter. Explicitly, let μ, ν, and θ be fractions defined as follows: μ = the fraction of catch removed prior to natural mortality; ν = the fraction of total mortality that occurs prior to spawning; θ = the fraction of total mortality that occurs prior to indexing the population. These parameters are built into the following three hypotheses for C, S, and I:

$$\tau_t N(w,t) = \sigma[N(w,t) - \mu C(w,t)] - (1-\mu)C(w,t) \tag{3.1}$$

$$S(w,t) = (1-\nu)N(w,t) + \nu\tau_t N(w,t) \tag{3.2}$$

$$I(w,t) = q[(1-\theta)N(w,t) + \theta\tau_t N(w,t)]. \tag{3.3}$$

These hypotheses have similar biological interpretations. In (3.1), σ represents survival from natural mortality. This equation assumes that the fraction μ of the catch C is first removed from N and then the survival fraction σ is applied to the difference $N - \mu C$. The remaining fraction $1 - \mu$ of the catch C is then removed to give the surviving population $\tau_t N$. Similarly, (3.2) assumes that the fraction $1 - \nu$ of the population N spawns before mortality and the remaining fraction ν spawns after mortality. In (3.3) the parameter q is a constant of proportionality between the actual population and the value of the index. The indexed population in (3.3) is assumed to be the sum of two parts, a fraction $1 - \theta$ of the population prior to mortality and the remaining fraction after mortality.

In practice, the timing parameters μ, ν, and θ would be specified by the modeler to conform with known circumstances in the fishery. For example, the choices

$$\mu = 1,\ \nu = 1,\ \theta = 0 \tag{3.4}$$

imply that catch takes place prior to natural mortality (e.g. early in the year), that spawning occurs subsequent to all mortality (e.g. late in the year), and that the index $I(w,t)$ reflects the entire initial population prior to all mortality. Although these are perhaps the simplest choices, (3.1)–(3.3) are flexible enough to cover most practical circumstances. In some cases, it may be necessary to allow the timing parameters to vary from year to year. Nothing essential is lost, for example, by writing μ_t in place of μ, provided that μ_t is presumed known for each year t.

The approach taken in (3.1)–(3.3) differs somewhat from historical methods. In particular, an extensive set of alternatives exist for (3.1), based on the classical coefficients of fishing and natural mortality, F and M, respectively, where $\sigma = e^{-M}$ and $\tau = e^{-F-M}$. For example, assuming that fishing and natural mortality occur simultaneously throughout the year, it can be shown (Appendix B) that

$$\mu = \frac{F(1-e^{-M}) - Me^{-M}(1-e^{-F})}{F(1-e^{-M})(1-e^{-M-F})}. \tag{3.5}$$

This rather complex expression can be shown (Appendix B) to reduce to the simple approximation

$$\mu \cong \frac{1}{1+\sqrt{\tau}} \tag{3.6}$$

when F and M are close. In particular, when fishing and natural mortality are equal ($F = M$ and $\tau = \sigma^2$), both (3.5) and (3.6) reduce to

$$\mu = \frac{1}{1+\sigma}. \tag{3.7}$$

The results (3.5)–(3.7) are included here primarily to relate the new assumption (3.1) to classical theory. Something useful, however, comes from the comparison. Since $0 < \tau < 1$, (3.6) suggests that μ must lie between 0.5 and 1.0 if fishing and natural mortality occur together throughout the year. In some cases, it might be interesting to test the hypothesis that fishing and natural mortality are approximately equal, in which case (3.7) could be used to define a model in which the unknown parameter σ directly determines μ.

To apply assumptions (3.1)–(3.3) in a biomass model, it is

TABLE 2. A composite model for the data I_t^*, C_t^*, and X_t.

[A1] $$N_t^* = \frac{I_t^* + q\theta[1 - \mu(1 - \sigma)]C_t^*}{q[1 - \theta(1 - \sigma)]}$$

[A2] $$S_t^* = [1 - \nu(1 - \sigma)]N_t^* - \nu[1 - \mu(1 - \sigma)]C_t^*$$

[A3] $$R_{t+1}^* = \sum_{a=k}^{K} \pi_a F(S_{t+1-a}^*)$$

[A4] $$N_{t+1}^* = R_{t+1}^* + \frac{X_t'}{X_t}[\sigma(N_t^* - \mu C_t^*) - (1 - \mu)C_t^*]$$

[A5] $$I_{t+1}^* = q\Big([1 - \theta(1 - \sigma)]N_{t+1}^* - \theta[1 - \mu(1 - \sigma)]C_{t+1}^*\Big)$$

necessary to convert them to biomass equations. Multiply each equation by w and integrate from V to V_∞ to obtain

(3.8) $$\tau_t N_t^* = \sigma[N_t^* - \mu C_t^*] - (1 - \mu)C_t^*$$

(3.9) $$S_t^* = (1 - \nu)N_t^* + \nu\tau_t N_t^*$$

(3.10) $$I_t^* = q[(1 - \theta)N_t^* + \theta\tau_t N_t^*],$$

respectively, from (3.1)–(3.3). Using (3.8), one can eliminate τ_t from (3.9)–(3.10). This gives

(3.11) $$S_t^* = [1 - \nu(1 - \sigma)]N_t^* - \nu[1 - \mu(1 - \sigma)]C_t^*$$

(3.12) $$I_t^* = q\Big([1 - \theta(1 - \sigma)]N_t^* - \theta[1 - \mu(1 - \sigma)]C_t^*\Big),$$

respectively, from (3.9) and (3.10).

To summarize briefly, I have introduced the three assumptions (3.1)–(3.3) and derived several results. In particular, equations (3.8), (3.11), and (3.12) express τ_t, S_t^*, and I_t^*, respectively, in terms of N_t^* and C_t^*. These three equations, together with moment equations derived earlier, provide the basic components for a variety of possible fishery models.

3B. A Simple Composite Model

The first question to ask in constructing any model is: what data are available? Data complexity governs model complexity, and, in the present context, the simplest model is based on the availability of the following times series:

(3.13) $$I_t^*, C_t^*, X_t.$$

For example, I_t^*, and C_t^* could represent catch per unit effort and catch, respectively, where the mean fish weight X_t is also presumed known from historical catch samples. In cases where the time series X_t is not known, it may be adequate to make the assumption (2.23) that $X_t = X$, where X is a typical fish weight determined from practical experience with the fishery. In this sense, the constant X could even be treated as a parameter, and the model could be tested for sensitivity to the choice of X. Essentially, then, the data (3.13) are equivalent to traditional catch and effort data. Other interpretations are possible, however. For example, I_t^* might be a spawn index used as an indicator of adult biomass.

Table 2 presents a composite model for the data (3.13). The model's five equations are based on equations from this paper, as listed in Table 3. For example, [A2] and [A5] come from (3.11) and (3.12), respectively, that is, from the timing assumptions related to spawning and indexing. Similarly, [A1] comes from (3.12), where that equation is solved for N_t^*. [A3] is the recruitment hypothesis (1.26). The main theoretical result used in Table 2 is the first-order moment equation (2.18). This, together with the survival equation (3.8), leads to the key equation [A4].

TABLE 3. Text source(s), input, and output for each model equation in Table 2. The absence of a subscript on an input or output variable indicates a time prior to $t + 1$.

Model	Text source(s)	Input	Output
[A1]	(3.12)	I^*, C^*	$\rightarrow N^*$
[A2]	(3.11)	C^*, N^*	$\rightarrow S^*$
[A3]	(1.26)	S^*	$\rightarrow R_{t+1}^*$
[A4]	(2.18), (3.8)	X, C^*, N^*, R_{t+1}^*	$\rightarrow N_{t+1}^*$
[A5]	(3.12)	N_{t+1}^*, C_{t+1}^*	$\rightarrow I_{t+1}^*$

Equations [A1]–[A5] are designed to predict I_{t+1}^* from C_{t+1}^* and data (3.13) at times prior to $t + 1$. Table 3 outlines the basis for this prediction by showing the input and output for each equation. Explicitly, the calculation would proceed as follows.

Step 1: Use [A1] and [A2] sequentially to compute S^* at times $t + 1 - K, t + 1 - (K - 1), \ldots, t + 1 - k$.

Step 2: Use the results from step 1 in [A3] to compute R_{t+1}^*.

Step 3: Compute N_t^* from [A1]. Use this result and the value of R_{t+1}^* from step 2 to calculate N_{t+1}^* from [A4].

Step 4: Finally, substitute the result from step 3 into [A5] to predict I_{t+1}^*.

In biological terms, steps 1 and 2 predict the recruitment in year $t + 1$ from past population sizes. Step 3 calculates the biomass in year $t + 1$ as the predicted recruitment plus the surviving biomass from year t, where the latter is adjusted for growth by the factor X_t'/X_t. Finally, step 4 relates the biomass in year $t + 1$ to the index value, and thus gives the desired prediction for I_{t+1}^*.

The model in Table 2 involves the parameters

(3.14) $$\mu, \upsilon, \theta, W, \rho, q, \sigma, G, H, \gamma, \delta, \pi_k, \ldots, \pi_K.$$

The first three of these (μ, υ, θ) are timing parameters, prescribed by the modeler. The growth parameters W and ρ are used only to calculate X_t' in [A4], and these may be known from auxiliary growth data. Furthermore, if the assumption

(2.23) applies, then only the ratio X'/X enters the model, and this may be available from sources external to the model data. The recruitment parameters G, H, γ, and δ are used in [A3] if, say, the recruitment function (1.31) is adopted. These would usually be restricted in some way; for example, the choices $\gamma = 1$ and $\delta = 0$ correspond to the Schaefer model. Finally, the fractions π_a $(a = k, \ldots, K)$ are constrained by (1.27*b*); consequently, π_K, say, can be determined from the other π's. In a typical case, then, the unknown parameters (3.14) would constitute a much shorter list, such as

$$(3.15) \quad q, \sigma, G, H, \pi_k, \ldots, \pi_{K-1}.$$

Even this list could be further reduced by assuming that the π's are restricted. For example, if the π's are presumed equal, then

$$\pi_a = 1/(K - k + 1);$$

that is, each π_a is determined, and only four parameters (q, σ, G, H) remain unknown.

3C. A More Complex Model

The model in Table 2 includes only rudimentary size data, the average weight X_t for each year t. It is even possible to bypass this requirement through the simplifying assumption (2.23) that $X_t = X$. A more complex and informative model can be tailored to a richer data set consisting of the time series

$$(3.16) \quad I_t^*, C_t^*, X_t, Y_t, Z_t$$

together with higher moment data

$$(3.17) \quad X_t^{(n)}, Y_t^{(n)}, Z_t^{(n)}$$

for $n \geq 2$. As described in connection with (2.10a)–(2.10b), the size data in (3.16)–(3.17) can be compiled from annual fish samples taken from the catch. This involves dividing each sample into two weight intervals, $[V, V')$ and $[V', V_\infty)$; consequently, both V and V' must be known in advance. Typically, V would be a size adequate to indicate full gear selectivity. Fish smaller than V might even be eliminated from the catch, as indicated in the discussion following the definition (1.21). Once V is determined, V' can be computed directly from the growth law (1.3), based on prior knowledge of W and ρ. In summary, the data (3.16)–(3.17) can be compiled from historical samples, provided that values of

$$(3.18) \quad V, W, \rho$$

are known before compilation begins.

The estimated quantities (3.18) can, however, be checked. Equations ⟨B1⟩ and ⟨B2⟩ in Table 1 suggest that a regression of Z_{t+1} on X_t should have slope ρ and intercept W and that a regression, constrained through the origin, of $Z_{t+1}^{(n)}$ on $X_{t+1}^{(n)}$ should have slope ρ^n. Therefore, preliminary analysis of the data (3.16)–(3.17) should involve the scatter plots

A: Z_{t+1} vs. X_t

B: $Z_{t+1}^{(n)}$ vs. $X_{t+1}^{(n)}$ for, say, $n = 2$ and $n = 3$.

All plots should indicate a linear trend in the data, and the two plots B should suggest lines though the origin. Furthermore, using the prior values (3.18) for W and ρ, the line

$$Z = W + \rho X$$

should be drawn on plot A and the line

$$Z^{(n)} = \rho^n X^{(n)}$$

should be drawn on each plot B $(n = 2, 3)$. If these lines do not appear to pass reasonably through the data, then it may be necessary to reestimate the values (3.18), recompile the data (3.16)–(3.17), and repeat the scatter plots A and B. When the parameters W and ρ are very poorly known, this entire procedure might be formalized numerically to give an algorithm for parameter estimation.

As explained at the end of Section 2, the higher moment data (3.17) are useful only to check or improve the estimate for ρ, and the data (3.16) are sufficient for a detailed parametric model. To build such a model, first define

$$(3.19) \quad \omega_t = R_t^*/N_t^*,$$

the fraction of total biomass in year t due to newly recruited fish. Since $N_t = R_t + P_t$, it follows from definitions (1.21)–(1.23) for the average weights X_t, Y_t, and Z_t that two equivalent expressions for the population N_t are

$$(3.20) \quad X_t^{-1}N_t^* = \omega_t Y_t^{-1}N_t^* + (1 - \omega_t)Z_t^{-1}N_t^*.$$

Solving for ω_t in (3.20) gives

$$(3.21) \quad \omega_t = \frac{Y_t}{X_t}\cdot\frac{Z_t - X_t}{Z_t - Y_t}.$$

Thus, if the data (3.16) are known, then the time series ω_t is available. Incidentally, notice that

$$(3.22) \quad Y_t < X_t < Z_t,$$

since (1) newly recruited fish are smaller than previously exploited fish and (2) the population average lies between the averages for these two extreme populations. The inequalities (3.22) can be used in (3.21) to prove that $0 < \omega_t < 1$.

Table 4 presents a model for the data (3.16), where the text source for each model equation [B1]–[B5] is given in Table 5. The logic underlying Tables 4 and 5 is similar to that for Tables 3 and 4, except that the time series ω_t is now available. This makes it possible to obtain two predictions for I_{t+1}^*, based on the recruited biomass R_{t+1}^* and the previously exploited biomass P_{t+1}^*, respectively. As in the previous model, equations [B1]–[B3] predict R_{t+1}^* from earlier population biomasses. Similarly, [B4] predicts P_{t+1}^* from the survival and growth of biomass in year t. These two results give two independent predictions of N_{t+1}^*:

$$(3.23) \quad N_{t+1}^* = R_{t+1}^*/\omega_{t+1}$$

$$(3.24) \quad N_{t+1}^* = P_{t+1}^*/(1 - \omega_{t+1});$$

and these, in turn, give the two predictions [B5a] and [B5b] for I_{t+1}^*.

The essential feature of this model is that size-structure data make it possible to distinguish new recruits from previously exploited fish. This means that two biological processes can be distinguished in the data: recruitment [B3] from various earlier years and the combined effects [B4] of growth and survival from a previous year. Specifically, in [B4] the factor X_t'/X_t accounts for growth and the expression in square brackets relates to survival. When using Table 4, the modeler can examine which prediction is better, that from [B5a] or [B5b]. This allows an objective assessment of which process, recruitment or combined survival/growth, is better defined by the data.

3D. Intuition

To be trustworthy, a model's results must appeal to common sense. An easy way to gain intuitive understanding is to exam-

TABLE 4. Composite model for the data I_t^*, C_t^*, X_t, Y_t, and Z_t. The time series ω_t is also presumed known, since it can be calculated from X_t, Y_t, and Z_t by (3.21).

[B1] $$N_t^* = \frac{I_t^* + q\theta[1 - \mu(1 - \sigma)]C_t^*}{q[1 - \theta(1 - \sigma)]}$$

[B2] $$S_t^* = [1 - \nu(1 - \sigma)]N_t^* - \nu[1 - \mu(1 - \sigma)]C_t^*$$

[B3] $$R_{t+1}^* = \sum_{a=k}^{K} \pi_a F(S_{t+1-a}^*)$$

[B4] $$P_{t+1}^* \doteq \frac{X_t'}{X_t}[\sigma(N_t^* - \mu C_t^*) - (1 - \mu)C_t^*]$$

[B5a] $$I_{t+1}^* = q\left(\frac{1 - \theta(1 - \sigma)}{\omega_{t+1}} R_{t+1}^* - \theta[1 - \mu(1 - \sigma)]C_{t+1}^*\right)$$

[B5b] $$I_{t+1}^* = q\left(\frac{1 - \theta(1 - \sigma)}{1 - \omega_{t+1}} P_{t+1}^* - \theta[1 - \mu(1 - \sigma)]C_{t+1}^*\right)$$

TABLE 5. Text source(s), input, and output for each model equation in Table 4. The absence of a subscript on an input or output variable indicates a time prior to $t + 1$.

Model	Text source(s)	Input	Output
[B1]	(3.12)	I^*, C^*	$\rightarrow N^*$
[B2]	(3.11)	C^*, N^*	$\rightarrow S^*$
[B3]	(1.26)	S^*	$\rightarrow R_{t+1}^*$
[B4]	(2.18), (3.8)	X, C^*, N^*	$\rightarrow P_{t+1}^*$
[B5a]	(3.12), (3.23)	$C_{t+1}^*, R_{t+1}^*, \omega_{t+1}$	$\rightarrow I_{t+1}^*$
[B5b]	(3.12), (3.24)	$C_{t+1}^*, P_{t+1}^*, \omega_{t+1}$	$\rightarrow I_{t+1}^*$

ine special cases. The models in Tables 2 and 4 are particularly simple when the timing parameters are given by (3.4). In this case, the prediction [A5] for I_{t+1}^* reduces to the single formula

$$(3.25) \quad I_{t+1}^* = q\sum_{a=k}^{K} \pi_a F\left[\frac{\sigma}{q}(I_{t+1-a}^* - qC_{t+1-a}^*)\right] + \sigma(X_t'/X_t)(I_t^* - qC_t^*).$$

Similarly, assuming (3.4), the predictions [B5a] and [B5b] reduce to

$$(3.26) \quad I_{t+1}^* = \frac{q}{\omega_{t+1}} \sum_{a=k}^{K} \pi_a F\left[\frac{\sigma}{q}(I_{t+1-a}^* - qC_{t+1-a}^*)\right]$$

$$(3.27) \quad I_{t+1}^* = \sigma(X_t'/X_t)(I_t^* - qC_t^*)/(1 - \omega_{t+1}),$$

respectively, where ω_{t+1} is calculated from (3.21). Interpretations of these results are now familiar: (3.26) relates to recruitment, (3.27) to growth/survival, and (3.25) to both processes combined.

Equations (3.25) and (3.27) suggest that I_{t+1}^* should correlate positively with I_t^* and negatively with C_t^*. Biologically, a large stock in year t should survive to become a large stock in year $t + 1$, while a large catch in year t should reduce the stock in year $t + 1$. In real data sets, I_t^* and C_t^* are often positively correlated because fishermen tend to take a large catch in years with high catch per unit effort. Consequently, I_{t+1}^* may share a positive correlation with *both* I_t^* and C_t^*, suggesting a negative value for q in (3.25) or (3.27). This situation may easily occur if the catch represents a fairly minor component of the fish population. Since natural mortality is highly variable, the catch in year t must have a significant negative effect on the available stock in year $t + 1$ if we are to distinguish fishing mortality from natural mortality. When the estimate for q turns out negative, it may be that the data show no evidence of stock reduction due to catch.

The above argument is incomplete, however, because the catch in year t influences the stock in two ways: through survival to year $t + 1$ and through recruitment to other future years. The model in Table 2 confounds these effects, while the more elaborate model in Table 4 has the potential to distinguish them. Since the effect of the catch is a fundamental issue in fishery management, there may be considerable value to the extra data needed to apply Table 4.

To gain even further insight into the models here, consider the case where (1) the fishery has little effect, that is, qC_t^* is small, (2) recruitment is constant ($F = G$), as in (1.33), and (3) the quantities X_t and ω_t are stable enough to be considered constants X and ω. Then, equations (3.25) and (3.27) reduce to

$$(3.28) \quad I_{t+1}^* = qG + \sigma(X'/X)I_t^*$$

$$(3.29) \quad I_{t+1}^* = \sigma(1 - \omega)^{-1}(X'/X)I_t^*,$$

respectively. These equations both suggest estimating the survival σ by regressing I_{t+1}^* on I_t^*. Essentially, (3.28) describes an autoregressive process, and the least squares slope estimator is known to be biased (Nahorski and Studzinski 1985; Walters 1985). By contrast, the regression (3.29) is *constrained through the origin*. Since I_t^* and I_{t+1}^* are approximately equal on average, (3.29) suggests that

$$(3.30) \quad \sigma(X'/X) = 1 - \omega.$$

The left side of (3.30) represents the usual survival and growth factors that govern the movement of the whole biomass into an exploited biomass one year later, and the right side is the fraction $1 - \omega$ of previously exploited biomass within the whole. This fraction reasonably relates directly to σ, as (3.30) suggests, because a population with high survival would typically have a large proportion of previously exploited fish. Thus, the time series ω_t is likely to be informative for the key parameter σ, and this suggests another potential value of the data needed to apply Table 4.

4. Generalized Cohort Analysis

The theory developed so far involves partitioning the population into two weight intervals, $[V, V')$ and $[V', V_\infty)$. These two groups of fish occur naturally in a model designed to capture the two processes of recruitment and survival. However, as discussed earlier in connection with the sequence of weights (1.10), the theory also suggests finer partitions of the population. The model can contemplate more processes as the number of groups increases. In particular, by increasing the number of distinct survival processes, the model can be designed to include size-dependent mortality.

The key idea for extending the theory here is to add weight intervals prior to $[V, V')$ and $[V', V_\infty)$. This requires a slight change of notation. Represent the weight of first recruitment by U, rather than V, and, by analogy with (1.10), define U_i recursively as follows:

$$U_0 = U \tag{4.1a}$$

$$U_i = (U_{i-1})'. \tag{4.1b}$$

To include g weight intervals prior to $[V, V')$, define V by

$$V = U_g. \tag{4.2}$$

Then, the population can be divided into $g + 2$ groups of fish with weights in the intervals

$$[U, U_1), \ldots, [U_{g-1}, U_g), [V, V'), [V', V_\infty). \tag{4.3a}$$

Surviving fish in group i grow into group $i + 1$ one year later, except for the final group of fish with weights above V'. These latter fish grow larger, of course, but remain in group $g + 2$. Incidentally, notice that if U_∞ is defined by letting i tend to ∞ in (4.1), then $U_\infty = V_\infty$, since $U_{i+g} = V_i$ (i.e. the two sequences agree beyond a certain point). Thus, the intervals (4.3a) can be written equivalently as

$$[U, U_1), \ldots, [U_{g-1}, U_g), [U_g, U_{g+1}), [U_{g+1}, U_{g+2}) \tag{4.3b}$$

where, for convenience, U_{g+2} is defined to be U_∞.

Most of this paper has been devoted to the last two groups $g + 1$ and $g + 2$ in (4.3) because these have the common feature that both grow into group $g + 2$ one year later. The moment equations in Table 1 require the assumption that mortality is not size selective for fish in these groups (i.e. fish weighing V or more). However, each of the first g groups (4.3) grows exclusively into the next group one year later, and general moment equations for each group transition can be derived without assuming a common mortality for all groups. In short, the theory requires uniform mortality only for the last two groups, and this key feature distinguishes models like those of Deriso (1980) and Schnute (1985) from multigroup models, such as those used in cohort analysis.

To derive a generalized cohort model from the hypotheses here, I must extend the notation somewhat. As before, let $N(w, t)$ denote a population density, where the range of w is now $[U, U_\infty)$. The main hypothesis (1.20) is replaced by

$$N(w', t + 1)\frac{dw'}{dw} = \tau_t(w)N(w, t) \tag{4.4}$$

where $\tau_t(w)$ is the step function

$$\tau_t(w) = \begin{cases} \tau_{it} & \text{if } U_{i-1} \le w < U_i \ (i = 1, \ldots, g) \\ \tau_t & \text{if } w \ge V. \end{cases} \tag{4.5}$$

Thus, survival τ_{it} from group i to group $i + 1$ during year t is indexed by both i and t, where $i = 1, \ldots, g$; however, for fish with weight $w \ge V$, the survival is designated τ_t as before. Essentially, (4.5) allows a distinct survival for each group, except that the final two groups are presumed to share a common survival.

Define the population, biomass, and average weight of fish in group i as follows:

$$Q_{it} = \int_{U_{i-1}}^{U_i} N(w, t)\,dw \tag{4.6}$$

$$Q_{it}^* = \int_{U_{i-1}}^{U_i} wN(w, t)\,dw \tag{4.7}$$

$$Y_{it} = Q_{it}^*/Q_{it}. \tag{4.8}$$

Similarly, define the nth-order central moment and the corresponding average for fish in group i by

$$Q_{it}^{(n)} = \int_{U_{i-1}}^{U_i} (w - Y_{it})^n N(w, t)\,dw \tag{4.9}$$

$$Y_{it}^{(n)} = Q_{it}^{(n)}/Q_{it}. \tag{4.10}$$

Finally, define $N_t, N_t^*, X_t, X_t^{(n)}$ exactly as before, with reference to the weight interval $[V, V_\infty)$. Thus, these quantities apply only to the combination of groups $g + 1$ and $g + 2$ in (4.3), *not* to the whole population. In terms of the quantities just defined, the complete system of moment equations for all groups in the population turns out to be

$$Q_{i+1,t+1} = \tau_{it}Q_{it} \tag{4.11}$$

$$Y_{i+1,t+1} = W + \rho Y_{it}. \tag{4.12}$$

$$Y_{i+1,t+1}^{(n)} = \rho^n Y_{it}^{(n)} \tag{4.13}$$

for $i = 1, \ldots, g$, and

$$Q_{g+2,t+1} = \tau_t N_t \tag{4.14}$$

$$Y_{g+2,t+1} = W + \rho X_t \tag{4.15}$$

$$Y_{g+2,t+1}^{(n)} = \rho^n X_t^{(n)}. \tag{4.16}$$

To understand this system of equations, notice first that the three equations (4.14)–(4.16) are identical to ⟨B0⟩–⟨B2⟩, respectively, in Table 1 with slightly altered notation. For example, $Y_{g+2,t+1}$ is the same as Z_{t+1}; both correspond to the average weight of the population in the weight interval $[V', V_\infty)$. Thus, the three equations (4.14)–(4.16) have already been proved. The proofs of (4.11)–(4.13) are almost identical, except that the ranges of integration must be changed in steps of the proof similar to (2.11)–(2.12) and (2.29)–(2.30). Conceptually, (4.11)–(4.13) describe the transition of moments from group i to group $i + 1$, just as (4.14)–(4.16) describe the transition from the combined groups $g + 1$ and $g + 2$ into group $g + 2$. The intuitive argument suggested by Fig. 1 still applies, except that the solid and broken curves in each panel must be confined to the appropriate weight ranges for groups i and $i + 1$, respectively.

A complete dynamic model from (4.11)–(4.16) requires only one additional assumption. Since the equations describe all possible transitions from one group to the next, it remains only to account for the population in the first group, that is, recruitment. The needed assumption, then, is already stated in

(1.26), provided that R_t and R_t^* are redefined in relation to the interval $[U, U')$, rather than $[V, V')$ as in (1.14)–(1.15). In current notation the average recruitment weight is Y_{1t}, rather than Y_t as before.

Readers familiar with cohort analysis will recognize in (4.11) the key equation of classical theory. If i represented age, then (4.11) would state that surviving fish of age i in year t reach age $i + 1$ in year $t + 1$. Here, the idea is generalized to refer to groups of fish with weights in the intervals (4.3). Indeed, the theory here includes age structure as a special case, because if the growth law is $w' = 1 + w$ (i.e. $W = 1$ and $\rho = 1$ in (1.3)), then w can be considered a measure of age.

Equations (4.11)–(4.16) tie together much existing theory. First, (4.11) generalizes cohort analysis with size-dependent mortality. Second, as proved in Section 2C, equations (4.14)–(4.15), which are equivalent to $\langle B0 \rangle$–$\langle B1 \rangle$ in Table 1, imply the models of Deriso (1980) and Schnute (1985). Finally, the higher moment equations (4.13) and (4.16) correspond, although somewhat imprecisely, to equations derived by Fournier and Doonan (1987).

A complete model with size-dependent mortality would require data compiled in a manner similar to (3.16)–(3.17), including data for each group of fish. The hypotheses (3.1)–(3.3) would need further elaboration to account for size-dependent mortality. For example, τ_t, σ, and q might all be allowed to vary among groups. These details are, however, primarily technical. The essential features of such a model are already evident in Table 4.

In applying any model, it is important to consider its limitations. As discussed at the start of Section 2, the model here is somewhat rigid because it assumes deterministic growth (1.3). Since growth is typically variable, group i does not always grow precisely into group $i + 1$ during one year. Growth variability in this context can be compared with errors in aging fish for an age-structured model. Both sources of variation lead to the problem of appropriate group definition. For example, in the size-structured model here, slow growth could be interpreted as high mortality; that is, if some fish in group i fail to grow into group $i + 1$ the next year, their absence from group $i + 1$ might seem to indicate mortality. The model's validity depends on the assumption that such errors tend to cancel statistically over a sufficiently long time series.

This paper has focussed primarily on theoretical linkages among historical models, based on underlying population size structure. To restrict the paper's scope, I have not discussed likelihood functions or estimation methods, obviously important topics for practical application. By putting the available methods into perspective, I hope to clarify their possibilities and limitations. Simple arguments, such as those in Sections 2D and 3D, can often be used to assess a model's potential for parameter estimation. In the end, an effective model should lead to a coherent explanation of the salient features of the data. This goal guides the search for mathematical simplicity. The moment equations derived here can provide not only analytical, but also conceptual, tools for rational stock assessment.

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Appendix A. Notation

This appendix describes and summarizes alphabetically (with Greek letters following Latin letters) all notation used in the paper. Equation numbers refer to places in the text where the symbol is defined or used. The paper involves two types of models, a two-group model with knife-edged selectivity in Sections 1–3 and a multigroup model with nonuniform selectivity in Section 4. I refer to these models (in this appendix only) as types I and II, respectively. Where necessary, the definitions below distinguish between model types.

a	subscript for age in an age-structured model; (1.1), (1.18)
a_0	parameter in the von Bertalanffy growth model (1.1) corresponding to theoretical age at weight 0
b	parameter in the autoregressive time series model (2.25)
c	constant in connection with the discussion (2.25)–(2.26) of autoregressive models
C_t	number of fish caught during year t
C_t^*	biomass of fish caught during year t; (3.8)

$C(w,t)$ density of fish caught during year t at weight w; (3.1)

F instantaneous fishing mortality; (3.5)

$f(w)$ function related to the distribution of weights in the fish population; (1.25)

$F(S^*)$ function defining the total biomass recruited from a stock biomass S^*; (1.25), (1.29)−(1.31)

g number of groups prior to the last two in a type II model; thus, the total number of groups is $g + 2$; (4.3)

G parameter in the recruitment function corresponding to the maximum possible recruitment; (1.31)−(1.32)

H parameter in the recruitment function corresponding to the stock biomass at maximum recruitment; (1.31)−(1.32)

i index for a sequence of weights U_i or V_i; group number in a type II model, where group i corresponds to fish in the weight interval $[U_{i-1}, U_i)$; (1.10), (4.1)

I_t population index in year t

I_t^* biomass index in year t; (3.10)

$I(w,t)$ density index in year t for the population at weight w; (3.3)

k youngest possible age of recruitment; (1.26)

K *first meaning*: a parameter in the von Bertalanffy growth model (1.1); *second meaning*: oldest possible age of recruitment; (1.26)

M *first meaning*: number of fish in a sample; (2.10a); *second meaning*: instantaneous natural mortality; (3.1)

M_z number of fish sampled with weight at least V'; (2.10b)

n superscript indicating the order of a moment; (2.1)−(2.6)

$\binom{n}{i}$ binomial coefficient; (2.14)

N_{at} number of fish aged a at the start of year t in an age-structured model; (1.18)

N_t number of fish with weight $w \geq V$ at the start of year t; (1.12)

N_t^* biomass of fish with weight $w \geq V$ at the start of year t; (1.13)

$N_t^{[n]}$ nth-order weight moment about the origin for fish with weight $w \geq V$ at the start of year t; (2.1)

$N_t^{(n)}$ nth-order central weight moment for fish with weight $w \geq V$ at the start of year t; (2.4)

$N(w,t)$ density of fish with weight w at the start of year t; (1.12)−(1.17), (1.19)−(1.20)

P_t number of previously exploited fish with weight $w \geq V'$ at the start of year t; (1.16)

P_t^* biomass of previously exploited fish with weight $w \geq V'$ at the start of year t; (1.17)

$P_t^{[n]}$ nth-order weight moment about the origin for fish with weight $w \geq V'$ at the start of year t; (2.3)

$P_t^{(n)}$ nth-order central weight moment for fish with weight $w \geq V'$ at the start of year t; (2.6)

q parameter, essentially a constant of proportionality, in the indexing equation (3.3)

Q_{it} number of fish in group i at the start of year t for a type II model; (4.6)

Q_{it}^* biomass of fish in group i at the start of year t for a type II model; (4.7)

$Q_{it}^{(n)}$ nth-order central weight moment in group i at the start of year t for a type II model; (4.9)

R_t number of newly recruited fish at the start of year t; these have weights in the interval $[V, V')$ for a type I model or $[U, U')$ for a type II model; (1.14)

R_t^* biomass of newly recruited fish at the start of year t; (1.15), (1.26)

$R_t^{[n]}$ nth-order weight moment about the origin for newly recruited fish at the start of year t; (2.2)

$R_t^{(n)}$ nth-order central weight moment for newly recruited fish at the start of year t; (2.5)

S_t reproductive stock population in year t

S_t^* reproductive stock biomass in year t; (1.26), (3.9)

$S(w.t)$ reproductive stock density at weight w in year t; (3.2)

t index for year t in a model; (1.12)−(1.20)

u typical fish weight; see the description of w, w', $\tilde{w}$

U weight at which fish are first selected by the gear in a type II model

U_i one of a sequence of weights defined by (4.1); in a type II model, group i is associated with fish in the weight interval $[U_{i-1}, U_i)$; (4.3)

U_∞ limit of the sequence U_i as $i \to \infty$; the same as V_∞ in a type II model; also denoted U_{g+2} for convenience in (4.3b)

V weight (1.6) at which fish are recruited to the fishery and selected by the gear in a type I model; the same as U_g in a type II model

V_i one of a sequence of weights defined by (1.10); see also (1.11)

V_∞ limit of the sequence V_i as $i \to \infty$; equal to $W/(1-\rho)$ if $\rho < 1$ or ∞ if $\rho \geq 1$

w typical fish weight

w' weight of a fish one year after its weight was w; (1.3)

$\tilde{w}$ weight of a fish one year prior to having weight w; (1.7)−(1.8)

w_a weight at age a; (1.1)

$w_i, \bar{w}$ weight of a single fish and average weight of all fish in a sample; (2.10a)

W parameter in the growth model $w \to w'$; (1.3)−(1.4)

W_∞ parameter in the von Bertalanffy growth model (1.1), corresponding to asymptotic fish weight

x_t observation in the autoregressive process (2.25)

X possible constant value for X_t below; (2.23)

X_t average weight of fish in the fully recruited population with weight $w \geq V$ during year t; (1.21)

$X_t^{(n)}$ average value of the nth central weight moment for fish with weight $w \geq V$ during year t; (2.7)

$\hat{X}_t^{(n)}$ sample estimate for $X_t^{(n)}$; (2.10a)

Y_t average weight of fish in the newly recruited population with weight in the interval $[V, V')$ during year t; (1.22)

$Y_t^{(n)}$ average value of the nth central weight moment for fish with weight in the interval $[V, V')$ during year t; (2.8)

Y_{it} average weight of fish in group i at the start of year t for a type II model; (4.8)

$Y_{it}^{(n)}$ average nth-order central weight moment in group i at the start of year t for a type II model; (4.10)

$z_i, \bar{z}$ see w_i, $\bar{w}$ above; (2.10b)

Z_t average weight of fish in the previously exploited population with weight $w \geq V'$ during year t; (1.23)

$Z_t^{(n)}$ average value of the nth central weight moment for fish with weight $w \geq V'$ during year t; (2.9)

$\hat{Z}_t^{(n)}$ sample estimate for $Z_t^{(n)}$; (2.10b)

α, β, γ parameters in the recruitment function (1.29)

δ recruitment parameter included to remove the requirement that $F(0) = 0$; extrapolated stock at zero recruitment; (1.30)−(1.31)

θ fraction of total mortality that occurs prior to indexing the fish population; (3.3), (3.10)

μ fraction of the catch removed prior to natural mortality; (3.1), (3.8)

ν fraction of total mortality that occurs prior to spawning; (3.2), (3.9)

π_a fraction of total recruitment from a single brood year that is newly recruited at age a, where new recruits have weights in the interval $[V, V')$; (1.26)−(1.27)

ρ parameter in the growth model $w \to w'$; (1.3)−(1.4)

σ fraction of the fish population that survives mortality by natural causes; (3.1), (3.8)

τ_{it} in a type II model, fraction of the population in group i that survives all mortality (fishing and natural) during year t; (4.5), (4.11)

τ_t fraction of the population that survives all mortality (fishing and natural) during year t; (1.19)−(1.20), (3.1), (3.8); in a type II model, τ_t applies only to the population in the weight interval $[V, V_\infty)$; (4.5), (4.14)

$\tau_t(w)$ total survival fraction in a type II model, for which mortality is size dependent; (4.5)

ω_t fraction of the total biomass in year t due to newly recruited fish; (3.19)−(3.21)

Appendix B. Proofs of (3.5)−(3.6)

In this appendix only, let t be a continuous variable ranging from 0 to 1, where t denotes time during the course of one year. Let $A(t)$ and $B(t)$ represent the population and catch, respectively, at time t resulting from an initial population N at time 0. If F and M are the coefficients of concurrent fishing and natural mortality, respectively, then $A(t)$ and $B(t)$ are governed by the system of equations

(B.1a) $dA/dt = -(F + M)A$

(B.1b) $dB/dt = FA$

(B.1c) $A(0) = N$

(B.1d) $B(0) = 0.$

Solving the system (B.1) for $A(t)$ and $B(t)$ gives

(B.2) $$A(t) = Ne^{-(F+M)t}$$

(B.3) $$B(t) = \frac{FN}{F + M}[1 - e^{-(F+M)t}].$$

If (3.1) is integrated with respect to w from V to V_∞, the result is

(B.4) $$A(1) = \sigma[N - \mu B(1)] - (1 - \mu)B(1)$$

in the notation here, since N is the initial population, $A(1)$ is the surviving population τN, and $B(1)$ is the catch for one year. Substitute (B.2)−(B.3) with $t = 1$ into (B.4) and then solve the result for μ to complete the proof of (3.5). Also, notice from (B.2) that since $\tau = A(1)/N$,

(B.5) $$\tau = e^{-F-M}.$$

To prove the approximate result (3.6), rewrite (3.5) as

(B.6) $$\mu = \frac{1}{1 - e^{-M-F}}\left[1 - \frac{Me^{-M}}{F}\,\frac{1 - e^{-F}}{1 - e^{-M}}\right].$$

Schnute (1977, equation (37)) cited essentially the following approximation:

(B.7) $$\frac{M}{F}\,\frac{1 - e^{-F}}{1 - e^{-M}} \cong e^{(M-F)/2}$$

when M and F are close. Taking account of (B.5), substitute (B.7) into (B.6) to obtain the approximate result

$$\begin{aligned}\mu &\cong \frac{1}{1 - \tau}\,[1 - e^{-(M+F)/2}] \\ &= \frac{1 - \sqrt{\tau}}{1 - \tau} \\ &= (1 + \sqrt{\tau})^{-1}.\end{aligned}$$

This proves (3.6).

Predation of Juvenile Pacific Salmon by the Common Merganser (*Mergus merganser*) on Eastern Vancouver Island. I: Predation during the Seaward Migration

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Wood, C. C. 1987. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. I: Predation during the seaward migration. Can. J. Fish. Aquat. Sci. 44: 941–949.

Predation of juvenile salmonids by the common merganser (*Mergus merganser*) was investigated during the period of seaward migration in two streams where fish populations are enhanced by spawning channels and hatcheries. Observation of foraging behaviour and crop-gullet contents indicated that, during this period, mergansers foraging on freshwater reaches of the streams ate juvenile salmonids almost exclusively whereas those foraging on tidal waters rarely ate salmonids. Maximum rates of salmonid mortality were estimated by assessing merganser abundance and the pattern of foraging activity on fresh versus tidal waters. Maximum mortality rate declined as fish abundance increased (i.e. mortality was depensatory) in all cases where the effects of prey size-selection could be ignored owing to an overwhelming abundance of one prey species. Bounds on maximum mortality rate by species for the entire migration period were computed under different hypotheses about the prey size-selection habits of mergansers; maximum mortality rate did not exceed 10% for any salmonid species over the entire seaward migration.

L'auteur a étudié la prédation des salmonidés juvéniles par le grand bec-scie (*Mergus merganser*) au cours de l'avalaison dans deux cours d'eau où les populations de poissons font l'objet d'une mise en valeur par chenaux de frai et installations piscicoles. L'observation du comportement de recherche de nourriture et l'examen du contenu des jabots et gosiers ont montré que, au cours de cette période, les becs-scies se nourrissant dans les zones d'eaux douces des cours d'eau consommaient presque exclusivement des salmonidés juvéniles tandis que ceux se nourrissant dans les eaux soumises aux marées en consommaient rarement. Les taux maximaux de mortalité des salmonidés ont été estimés à partir d'une évaluation de l'abondance des becs-scies et de leur mode de recherche de nourriture dans les eaux douces ou soumises aux marées. Le taux de mortalité maximal déclinait à mesure que l'abondance des poissons augmentait (mortalité inverse), ceci dans tous les cas où l'on pouvait ignorer les effets d'une sélection pour la taille des proies à cause d'une surabondance d'une espèce donnée de proies. Des limites du taux de mortalité maximal par espèce ont été calculées pour toute la période de migration et pour diverses hypothèses relatives à la taille des proies préférées par les becs-scies. Le taux de mortalité maximal n'a jamais excédé 10 %, ceci pour chacune des espèces de salmonidés et pour toute la période d'avalaison.

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The common merganser (*Mergus merganser*) is a large and efficient predator of juvenile salmonids; it is highly mobile and will congregate and nest near profitable feeding areas (Wood 1985, 1986). Not surprisingly, the merganser has long been regarded as a menace to sport fish populations (e.g. Leonard and Shetter 1936; Beach 1937; Huntsman 1941; Elson 1962). Despite its great potential as a predator of salmon, some investigators (e.g. Munro and Clemens 1937; Salyer and Lagler 1940) have emphasized that the merganser feeds more commonly on "coarse" fishes and only threatens salmon and trout populations under exceptional conditions. Salmonid enhancement facilities such as spawning channels and hatcheries usually create exceptional conditions where the density of juvenile salmon can be many times greater than found in nature. Thus, a new facet of the merganser predation controversy must be considered: does mortality due to mergansers decrease as salmon populations are enhanced because mergansers become swamped by prey (depensatory mortality), or does it increase because mergansers congregate in larger and larger feeding flocks (compensatory mortality)?

The impact of predation by mergansers on fishable salmon stocks will depend not only on the proportion eaten, but on the opportunities for compensatory growth and mortality during the subsequent life of surviving fish. For example, the survival of salmonids that rear in fresh water is usually limited by the amount of suitable habitat (Chapman 1962, 1965), particularly during periods of low flow (Marshall and Britton 1980) and over winter (Holtby and Hartman 1982; Tschaplinski and Hartman 1982). Predation on these fish early in the summer may have little consequence for the eventual size of the cohort migrating to sea the following spring. However, it is widely believed that ocean survival and growth are only weakly correlated with salmonid density under typical conditions (Larkin 1974; MacLeod 1977; Peterman 1978; but see Peterman 1984). Where this is true, any additional mortality of hatchery-reared smolt at release, or of fry emigrating from artificial spawning channels, will cause a roughly proportionate reduc-

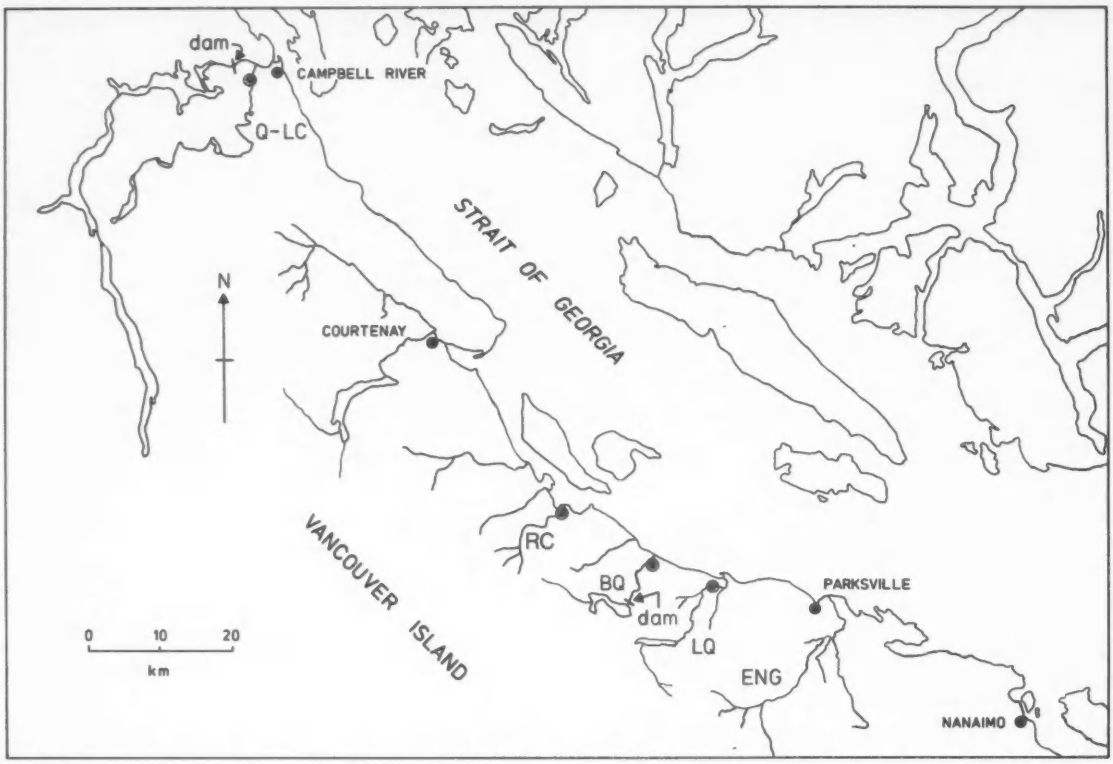

FIG. 1. Study area. Q-LC, Quinsam – lower Campbell River system; RC, Rosewall Creek; BQ, Big Qualicum River; LQ, Little Qualicum River; ENG, Englishman River. Encircled dots indicate site of spawning channel or hatchery.

tion in the abundance of returning adults. Hence, it is especially desirable to minimize freshwater predation on these cohorts.

In this paper, I examine potential salmonid mortility due to mergansers by monitoring the abundance of mergansers over a wide range of salmonid density. For the reasons already stated, I consider predation by adult mergansers only during the seaward migration of juvenile Pacific salmon — the period from late March to early July on Vancouver Island. The potential for predation on stream-resident salmonids (salmonid fry and parr) by merganser broods during June through September is examined in a companion paper (Wood 1987).

Study Area

Mergansers, glaucous-winged gulls (*Larus glaucescens*), Bonaparte's gulls (*L. philadelphia*), great blue herons (*Ardea herodias*), bald eagles (*Haliaeetus leucocephalus*), and belted kingfishers (*Megaceryle alcyon*) were censused on three neighbouring streams, the Big Qualicum (BQ) and Little Qualicum (LQ) rivers and Rosewall Creek (RC) (Fig. 1), at intervals of 1–4 d during the period of seaward migration, late March to early July, in 1980 and 1981. Spawning channels and/or hatcheries contribute to fish production on all streams. Physical data and salmon production statistics for each system, and details of the census procedure are described by Wood (1985, 1987).

Methods

Estimating Maximum Mortality

The average consumption of fresh fish by an adult merganser is about 0.4 kg/d (e.g. Wood and Hand 1985). Mergansers observed on fresh water fed almost exclusively on salmonids whereas those sighted on tidal waters fed only on other species (see Results). Census estimates of the relative abundance of mergansers in these two habitats indicated the proportion of time spent foraging in each. Although mergansers move freely between fresh water and tidal waters, it is equivalent, computationally, to assume that only birds sighted on fresh water consumed salmonids during that day. Evidence is presented in the following section to support this assumption.

Maximum daily mortality of salmonids was computed by assuming that all mergansers sighted on fresh water fed to satiation exclusively on salmonids (equation (1)):

$$(1)\quad \%\ \text{maximum mortality of species } i = (p_i NC / w_i n_i) \times 100$$

where N is the number of mergansers on fresh water, C is consumption per bird per day (0.4 kg), n_i is the number and w_i, the average weight of prey species i migrating downstream that day, and p_i is the proportion of species i in the diet. Where a single prey species was overwhelmingly abundant compared

with alternative prey, I assumed that $p_i = 1$. I estimated the maximum mortality rate for single days and plotted these values against prey density (n) to determine whether mortality due to mergansers was depensatory or compensatory. Where this was not possible because $p_i < 1$, I computed bounds on maximum mortality rate for the entire period of seaward migration by making three alternative assumptions: first, that prey items were taken in proportion to their density, regardless of size; second, that prey items were selected in proportion to their representation by biomass; and third, that selection was proportional to cross-sectional area as seen against a background (after Wood and Hand 1985). For large fish (smolt), these assumptions provide lower and upper bounds and an intermediate or "best" estimate, respectively. In general:

$$(2)\quad p_i = v_i n_i / \Sigma_i v_i n_i$$

where $v_i = 1$ implies selection in proportion to density, $v_i = w_i$ implies selection in proportion to biomass, and $v_i = (l_i/l_f)^2$ under the cross-sectional area model in which l_i = length of prey species i and l_f = 3.8 cm, the length of a chum salmon (*Oncorhynchus keta*) fry used as a standard for comparison. These relationships are illustrated in Wood (1985). Estimates of merganser abundance for the intervals between census days were obtained by interpolation. Estimates of fry density were obtained from counting fences on BQ and LQ (Department of Fisheries and Oceans, Big Qualicum River Development Project, Qualicum Bay, B.C., unpubl. data). Daily estimates of smolt densities from diving surveys in BQ were provided by Dr. P. Mace (Department of Fisheries and Oceans, Halifax, N.S., pers. comm.); some of these data are available in her 1983 report.

Results

Location of Foraging Activity

Mergansers observed while foraging on tidal waters rarely ate salmonids; intertidal fishes, predominantly sculpins (Cottidae) and blennies (Stichaeidae or Pholidae), comprised the majority of their diet. In contrast, those observed while foraging on fresh water on BQ fed almost exclusively on salmonids. Fish remains were obtained from the crops and gullets of 14 mergansers captured on freshwater reaches of the BQ system and treated with an emetic drug (see Wood 1985 for details of treatment). Of these samples, only two revealed evidence of nonsalmonid fishes; both contained a mixture of marine species and salmonid fry. Freshwater sculpins are also eaten (Munro and Clemens 1937), but probably only when salmonids are relatively scarce. Only three sculpins (probably *Cottus asper* or *Cottus aleuticus*) were eaten by mergansers foraging in experimental field enclosures over a 5-wk period, contributing <0.5% of all prey eaten, despite the fact that these fish were often more numerous within the enclosures than the salmonid prey which accounted for the balance of the diet (Wood and Hand 1985). Accordingly, estimates of predation on salmonids in the following analyses are based solely on freshwater counts.

Merganser density was highest on the lower kilometre of the BQ system throughout the downstream migration in both 1980 and 1981 (Fig. 2). This is the zone immediately below the BQ hatchery. Density declined farther upstream such that, at most, an additional 10–15% of the total count to 5 km would be expected on the remaining headwaters below the dam at Horne Lake. Foraging activity was not correlated with time of day or tide height between 05:00 and 21:00 PST (Wood 1984). Moreover, the proportion of the total river system count foraging on tidal waters did not change significantly with time of day ($p > 0.10$, Wilcoxon–Mann–Whitney test) or tide height ($p > 0.40$, Wilcoxon–Mann–Whitney test). Hence, I conclude that the dispersion of mergansers on fresh water as opposed to tidal waters also reflects the dispersion of foraging activity within the river system throughout the day.

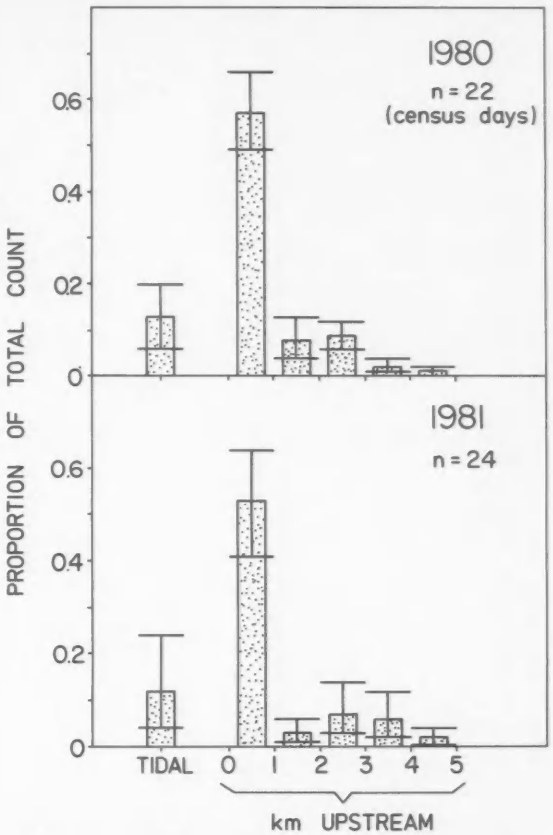

FIG. 2. Distribution of mergansers on the Big Qualicum River, April–June 1980 and 1981. The 95% C.I. were calculated from arcsine-transformed data. The hatchery is located 1.3 km upstream from the river mouth.

Estimates of Mortality

Trends in the abundance of mergansers in relation to the availability of juvenile salmon were similar in 1980 and 1981 on BQ (Fig. 3). Compared with BQ, mergansers were relatively more abundant on tidal waters than on fresh water on the LQ system (Fig. 4). This is attributed to differences in juvenile salmonid production in the two rivers (Wood 1985). The fish availability index is based on the intermediate size-selection assumption and is intended to represent feeding conditions from a merganser's perspective.

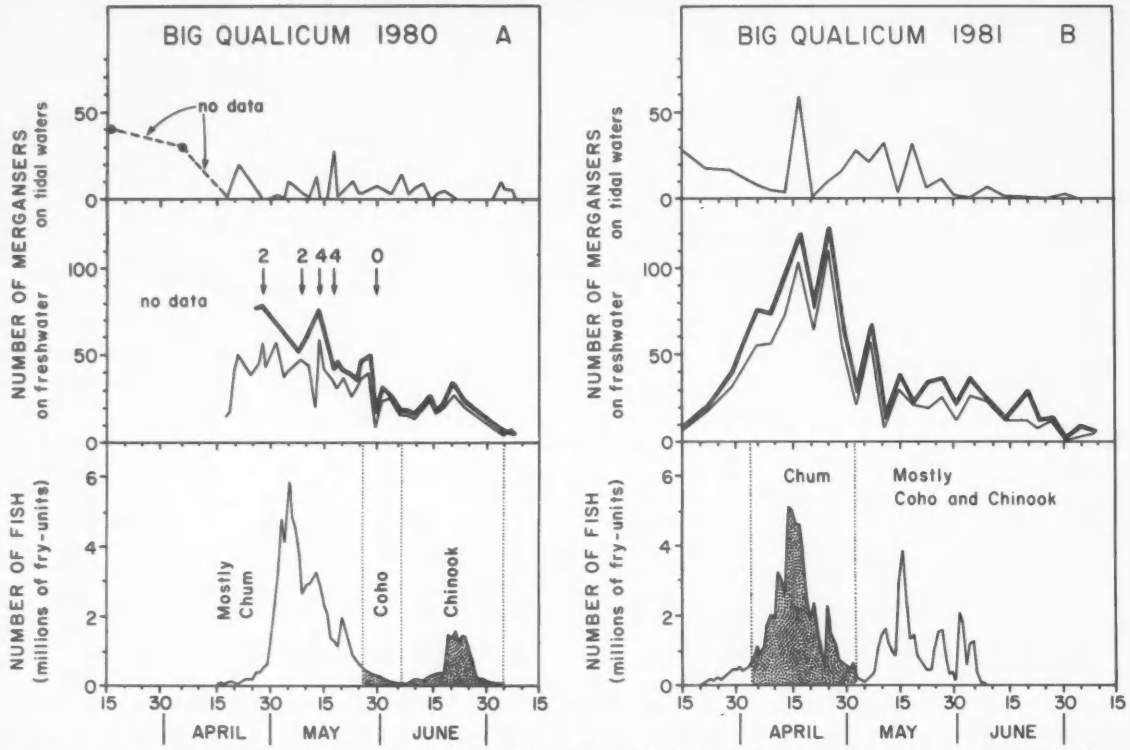

FIG. 3. Trends in the abundance of mergansers on fresh water and tidal waters of the Big Qualicum River system in (A) 1980 and (B) 1981 in relation to the availability of juvenile salmon migrating downstream. Freshwater counts are summarized for the lower 2.5 km (light line) and 5 km (heavy line); numbers above arrows indicate the number of mergansers observed on the remainder of the stream (below the dam) for occasions when a complete census was undertaken. Fish availability is expressed in fry-units under the intermediate size-selection assumption such that a chum salmon fry is 1 fry-unit. Stippled segments of trend in fish availability indicate data used for mortality computations in Fig. 5.

The bounded estimates for mortality rate on each species over the entire migration period in BQ (Table 1) were computed by assuming that mergansers on fresh water fed to satiation exclusively on salmonids during the seaward migrations. Thus, each estimate represents a maximum mortality rate under a different assumption about prey-size selection. The maximum estimates of mortality rate are probably good estimates of the actual mortality rate when fish availability was very high, for example, following hatchery releases. The size-selection assumption is critical where emergent chum fry (0.3–0.4 g) and large steelhead (*Salmo gairdneri*) smolt (45–90 g) are vulnerable simultaneously. In this case, maximum mortality estimates for steelhead smolt with selection in proportion to biomass are 2 orders of magnitude greater than for selection in proportion to density. For other size comparisons, the estimates are more robust. In no case did the estimated mortality rate exceed 10% due to predation by mergansers. Under the intermediate size-selection hypothesis, cohorts released or migrating early in the year (April – early May) sustained maximum losses in the range of 0.3–7.2% whereas those released in late May – early July suffered maximum losses of only 0.8–1.5%. It should be noted that these estimates are based on census counts to 5 km upstream of the river mouth. Evidence from patterns of merganser abundance on the lower 5 km (Fig. 2), and from five censuses of the entire stream below the dam (arrows in Fig. 3A), suggests that the total freshwater count, and thus the total mortality rate, is likely to be 10–15% higher than computed for Table 1.

Estimates of maximum mortality are most reliable for situations where the prey can be regarded as a single species by virtue of its overwhelming abundance relative to other prey (i.e. $p_i \approx 1$). These situations occurred during the chum fry migrations on the BQ and LQ systems, both of which have artificial spawning channels and fry enumeration facilities, and during the coho (*O. kisutch*) and chinook (*O. tshawytscha*) smolt releases from the BQ hatchery in 1980 (see stippled segments of juvenile salmon production in Fig. 3 and 4). Unfortunately, the coho and chinook releases overlapped in BQ during 1981 so that the problem of size-selection cannot be ignored.

Despite the aggregative response exhibited by mergansers (Wood 1985), the mortality rate always decreased with increasing fish density (Fig. 5). The effect of aggregation is apparent, however, because point estimates of maximum daily mortality rate lie along a trajectory that is more nearly linear and whose slope is less negative than would be expected, were merganser density constant (solid lines). The aggregative response also declines over the course of the season; estimates fall closer to the line representing constant density as the season progresses from April–May (Fig. 5A and 5B) to May–June (Fig. 5C) and finally to June–July (Fig. 5D).

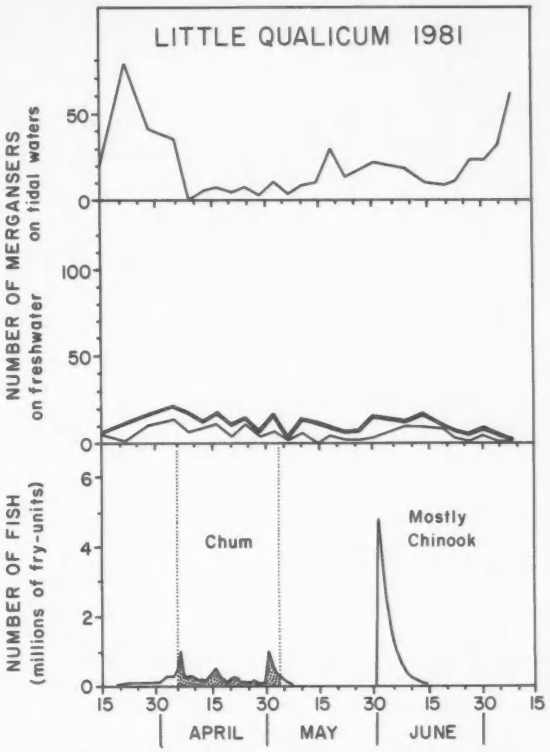

FIG. 4. Trends in the abundance of mergansers on fresh water and tidal waters of the Little Qualicum River system in 1981 in relation to the availability of juvenile salmon migrating downstream. Freshwater counts are summarized for the lower 2.5 km (light line) and 5 km (heavy line). Fish availability is expressed in fry-units under the intermediate size-selection assumption such that a chum salmon fry is 1 fry-unit. Stippled segments of trend in fish availability indicate data used for mortality computations in Fig. 5.

Effect of Size and Spacing of Fish Releases

I investigated the effect of size and spacing of fish releases on mortality rate in simulation experiments using the equilibrium aggregation model described by Wood (1985). The parameter values in these simulations were identical to those used in other simulations for BQ where predicted trends in merganser abundance compared favourably with observed trends (e.g. fig. 10 in Wood 1985). I assumed that the number of fish remaining in fresh water following a release decreased exponentially with time so that the proportion remaining in fresh water after 1 d is exp $(-z)$. Two plausible parameter values were tested: $z = 0.4$ and $0.6/\mathrm{d}$ corresponding to mean residence times of 2.5 and 1.7 d, respectively. In each scenario, the manager must release 50000 smolt within 20 d. He can do this by allowing a single large release or up to 10 smaller (equal-sized) releases spaced as far apart as possible within the 20 d.

Of these trials, the single release proved superior to all other schedules (Fig. 6A). This is because most fish reach the sea before the merganser aggregation reaches its equilibrium size. When releases are small and numerous, equilibrium is achieved quickly following each release and the trade-off between the magnitude of the equilibrium aggregation and the number of times this occurs is roughly equivalent; consequently, the mortality rate curve reaches an asymptote. In another trial, the effect of spacing was evaluated for equal-sized releases (Fig. 6B). Again, the single large release (i.e. 0-spacing) is the best strategy. Because some time is required for the aggregation to build to equilibrium, whereas fish density declines monotonically following release, the mortality rate will always be low initially and then increase dramatically as fewer and fewer fish remain vulnerable. In other words, fish exhibiting longer residence times following release are at far greater risk than those that emigrate quickly.

Discussion

These estimates of maximum mortality rate due to mergansers hinge on a number of assumptions regarding the location of foraging activity, diet, and size-selection of prey. Before drawing conclusions about the impact of merganser depredations, it is prudent to consider whether these assumptions are justified and how well they can be generalized to other situations.

First, is it reasonable to ignore predation of juvenile salmonids by mergansers foraging on estuaries? There is a great deal of information available regarding gut contents of mergansers feeding on a wide variety of habitats. Virtually all these studies (White 1936, 1937, 1957; Munro and Clemens 1936, 1937; Salyer and Lagler 1940; Lindroth 1955; Latta and Sharkey 1966; Timken and Anderson 1969; Miller 1973; Alexander 1979) indicate that mergansers eat salmonids wherever they are conspicuous relative to other species. In particular, White (1939) observed that the proportion of salmonids comprising the diet of red-breasted mergansers declined from 100 to 73 to 12% for birds killed on the headwaters, lower reaches, and upper estuary, respectively, of the Margaree River, Nova Scotia. These data are consistent with my limited observations of diet among common mergansers on Vancouver Island streams. In their review article, Salyer and Lagler (1940) concluded that mergansers threaten salmon populations only when concentrated on productive salmon-rearing waters. These authors also reported that mergansers wintering on lakes and streams in Michigan tend to congregate on the lower reaches of rivers, as observed on Vancouver Island during the spring and summer.

Second, assumptions about daily consumption and size-selection of prey require substantiation. White (1957) reported the average daily consumption of a tame (but not captive) male merganser to be 440 g or 38% of body weight; four other captive birds in his study averaged 380 g/d or 30% of body weight. Other studies with captive birds suggest lower consumption rates (ranging from 19 to 26% of body weight, Latta and Sharkey 1966; Miller 1973), but all these birds lost weight in captivity. Indeed, Miller concluded that 450 g/d was reasonable (on metabolic grounds) for wild, active mergansers. Daily consumption was estimated to be 290–450 g or 20–40% of body weight, depending on sex, by extrapolation from ingestion rates of wild birds feeding on coho smolt of known size (Wood and Hand 1985). Thus, the estimate of 400 g/d, used in the present calculations, seems justified.

Less information is available regarding the size-selection of prey by mergansers. In general, mergansers appear to choose a disproportionate number of large fish compared with sizes typically available (Salyer and Lagler 1940; Elson 1962;

TABLE 1. Maximum estimates of salmonid mortality rate (%) due to adult mergansers during seaward migration in the Big Qualicum River, April 15–July 15, 1980 and 1981.

Species	Size-selection assumption: Density $v_i = 1$ 1980	Density $v_i = 1$ 1981	Intermediate $v_i = (l_i/l_j)^2$ 1980	Intermediate $v_i = (l_i/l_j)^2$ 1981	Biomass $v_i = w_i$ 1980	Biomass $v_i = w_i$ 1981	Range
Emergent fry (chum, coho) (0.33 g)	3.8	6.0	3.5	5.7	3.3	5.2	3.3–6.0
Reared chum fry (0.9 g)	—	6.9	—	7.2	—	8.4	6.9–8.4
Reared chinook smolt (6.0 g)	1.3	0.9	1.2	0.8	1.2	0.7	0.7–1.3
Reared coho smolt (17 g)	1.2	0.8	1.5	1.0	1.7	1.1	0.8–1.7
Reared steelhead smolt (45–90 g)	<0.1	<0.1	0.3	0.8	2.1	5.6	<0.1–5.6

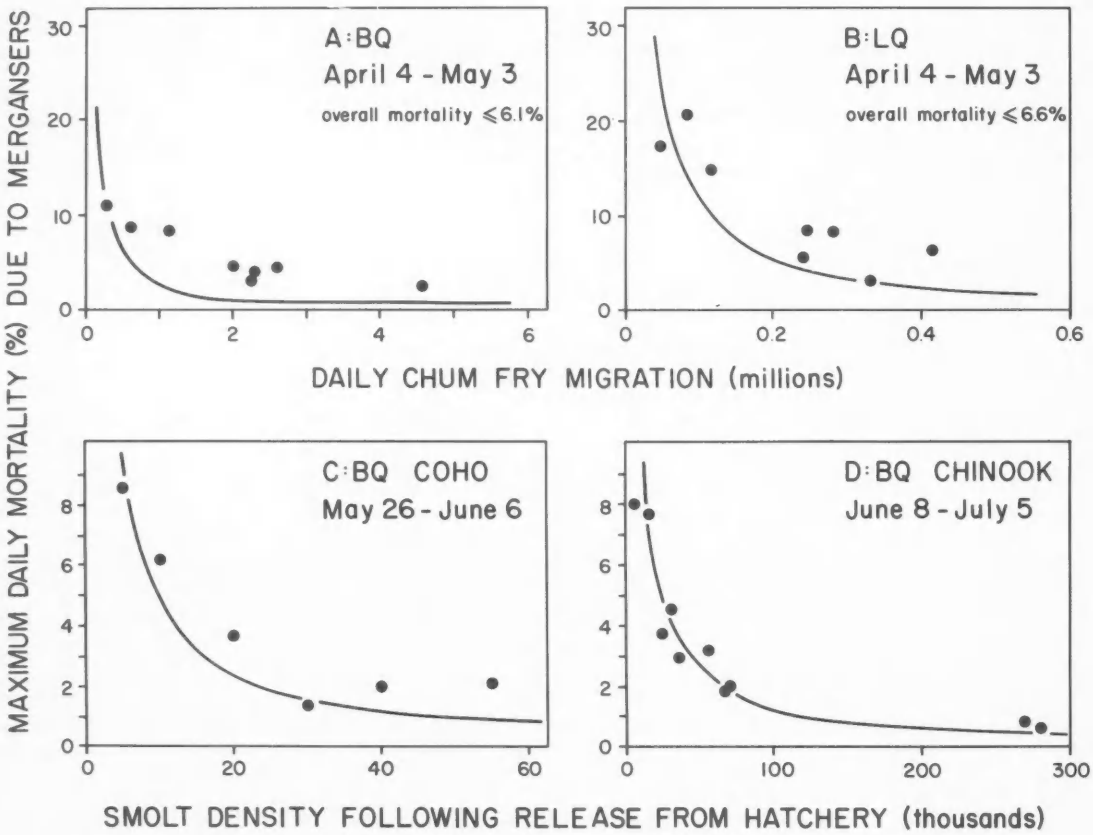

FIG. 5. Relationships between percentage mortality and salmonid density over periods when a single species was very abundant relative to alternative prey. (A) Peak chum fry migration in Big Qualicum River (1981); (B) peak chum fry migration in Little Qualicum River (1981); (C) coho smolt migration in Big Qualicum River (1980); (D) chinook smolt migration in Big Qualicum River (1980). Dots indicate daily estimates of maximum mortality; solid lines indicate expected relationship if merganser density remained constant. Overall estimates of maximum mortality are computed by interpolation from daily estimates.

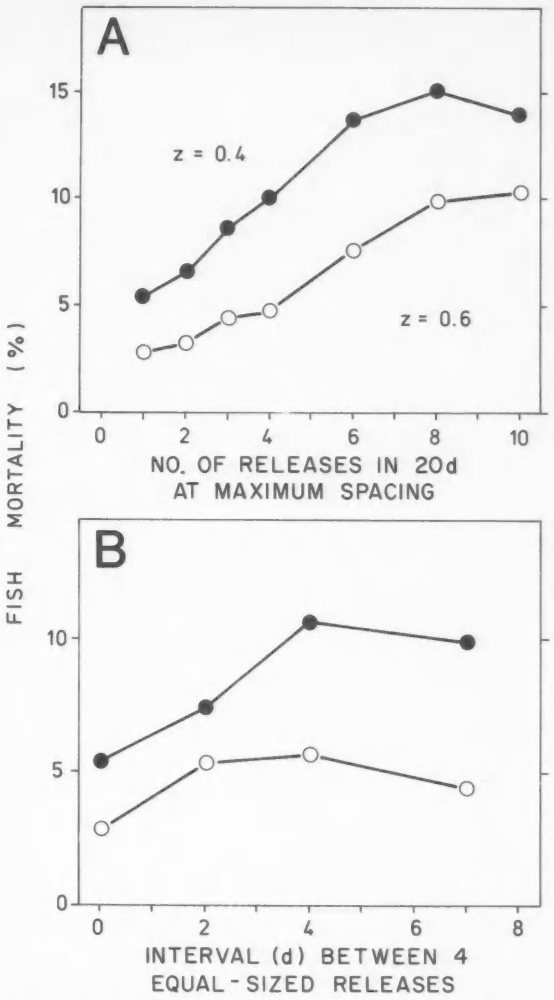

FIG. 6. Relationships between mortality expected due to merganser aggregation and the (A) size and (B) spacing of releases of hatchery fish.

Alexander 1979). Mergansers also selected coho smolt weighing approximately 40 g over coho fry weighing about 2 g when both were stocked in large, relatively natural stream enclosures (Wood and Hand 1985). Selection in the latter study could be explained in terms of differential visibility of prey which justified the intermediate size-selection assumption in the present analysis. Mergansers given a choice of trout ranging from 10 to 20 cm in small tanks where differential visibility could be ignored exhibited a preference for fish of smallest girth (Latta and Sharkey 1966). Swennen and Duiven (1977) also concluded that three species of alcids, the guillemots (*Uria aalge*), razorbills (*Alca torda*), and puffins (*Fratercula arctica*), selected fish based on girth rather than length and preferred fish about half the maximum size that could be swallowed. Evidently, selection of large fish in natural situations cannot be interpreted as preference in the strict sense. It is also clear that the intermediate size-selection assumption is superior to the alternatives at either extreme. Nevertheless, the problem deserves further study. Size differences among species and age classes of emigrating salmonids can be very large, and the size-selection assumption is critical for estimating mortality rate when many size classes are vulnerable simultaneously. It might be possible to buffer valuable species by releasing them in the presence of cheaper and more vulnerable species.

Juvenile salmon are vulnerable to predation for a period of days, or at most, weeks, during their downstream migration. A predatory species must be very abundant to inflict appreciable mortality on large populations which are at risk for so short a time. Mergansers rank among the largest (in terms of appetite) and most efficient predators of juvenile salmon; what is more, they are relatively common and congregate wherever salmon density is high. Despite this, the overall mortality rate due to mergansers was depensatory — mergansers were simply swamped by the output from spawning channels and hatcheries.

The mortality rate due to mergansers is very unlikely to have exceeded 8% for any particular stock during downstream migration where size-selection effects can be ignored. This represents a substantial number of fish, but in view of the difficulty and expense of controlling merganser abundance on salmon streams (Elson 1962; Miegs and Rieck 1967; Anderson et al. 1985) — not to mention justifiable concerns on esthetic and ecological grounds (Anderson et al. 1985) — it is probably more reasonable to accept these losses to mergansers. Where necessary, losses can be mitigated simply by increasing hatchery production by 5–10%, since mortality is depensatory.

The hatchery manager must release a large number of reared fish over a short season. Due to the number of fish involved and the efficiency with which mergansers capture salmonids at even low density (Wood and Hand 1985), it is inevitable that mergansers will be able to feed to satiation under any feasible release schedule. If merganser density were constant (i.e. independent of fish density) and other things equal, the best release strategy is clear: all fish should be released simultaneously so as to allow mergansers the shortest possible time in which to gorge. Unfortunately, salmonids released from rearing ponds do not leave the stream immediately or predictably (Mace 1983), and mergansers do congregate wherever feeding opportunities are favourable. Given these constraints, it is not so obvious which release schedule will minimize mortality by mergansers. It seems plausible that a series of small releases may attract fewer predators than a single large release. However, the simulation results in Fig. 6 demonstrate that merganser predation could be minimized by reducing the period over which fish are vulnerable (i.e. single, large, forced releases) and by delaying fish releases as much as possible. Other considerations will constrain a manager's ability to adopt these tactics but the trade-offs can be evaluated. The overall success of such tactics will depend on the ability of young salmon to disperse once at sea and upon the actions of estuarine and marine predators. It is still essential to learn where bottlenecks exist (in terms of migrant survival) and whether these bottlenecks can be relieved rather than merely postponed to a subsequent stage of development.

It seems improbable that other fish-eating birds impose more serious mortality on juvenile salmon during their seaward migration in Vancouver Island streams. Herons, eagles, and kingfishers are all efficient predators with large appetites (Alexander 1979) but all were less common than mergansers

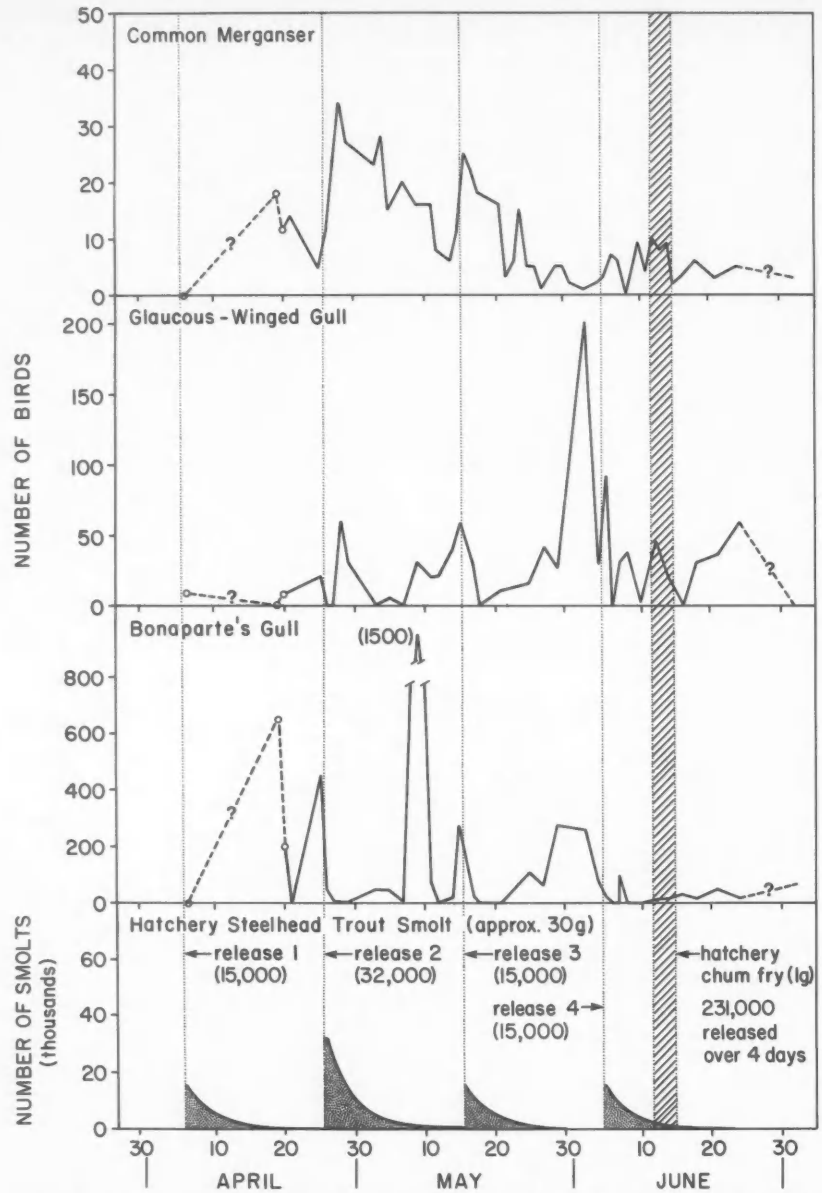

FIG. 7. Trends in the abundance of the three most common fish-eating birds on Rosewall Creek in 1980 following sequential releases of hatchery-reared steelhead trout smolt. Census area included the lower 1 km of fresh water and the estuary within a 0.5-km radius of the river mouth (not including Mud Bay). Estimation of smolt residence times is described in Wood (1985). Open symbols are minimum estimates due to incomplete census coverage of fresh water.

on eastern Vancouver Island streams. These species may cause significant mortality among stream-resident salmonids that are vulnerable for long duration, but their depredations are unlikely to be serious during the brief period of seaward migration in these coastal streams. Gulls, particularly Bonaparte's gulls and glaucous-winged gulls, are numerous and feed on juvenile salmon under favourable conditions following hatchery releases. However, gulls are opportunistic piscivores and with one exception, noted below, the distribution and size of gull flocks seemed to be unrelated to the downstream migration of salmon in the streams I have censused (e.g. Fig. 7). Mace (1983) documented an aggregation response by Bonaparte's gulls to the chinook smolt migrations through the BQ estuary over several consecutive years. But

BQ appears to be an exceptional case, perhaps because of the unusually high densities of chinook smolt released there; Mace found no evidence of aggregation in response to chinook smolt releases from the Capilano River hatchery during the same period. Even on BQ, mortality due to predation by gulls was depensatory.

Probably no single species of avian predator is capable of inflicting compensatory mortality on juvenile salmonids during their seaward migration. If this is true, it follows that predation by all fish-eating birds, acting in concert, must also be depensatory and that salmon populations cannot be regulated by avian predation during their seaward migration. The vulnerable period during migration is simply too short, at least for relatively small, coastal rivers. However, depensatory predation during seaward migration may help to maintain (temporarily) patterns of dominance among different year classes or populations of Pacific salmon (Ricker 1962; Larkin 1971). Salmon runs severely reduced by catastrophe or overfishing will experience higher mortality due to predators than populations near equilibrium, and hence, may take much longer to return to equilibrium abundance than expected. Similarly, depensatory mortality will favour survival of fish in unusually large runs and should provide bonuses for salmonid enhancement programs.

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Predation of Juvenile Pacific Salmon by the Common Merganser (*Mergus merganser*) on Eastern Vancouver Island. II: Predation of Stream-Resident Juvenile Salmon by Merganser Broods

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Predation of stream-resident juvenile salmonids by broods of the common merganser (*Mergus merganser*) was investigated in three streams on eastern Vancouver Island from 1980 to 1982. Daily fish consumption by merganser ducklings was estimated to range from 80% of body weight for ducklings at 10 d of age to 40% of body weight for those at 40 d of age. Merganser ducklings were never observed to eat juvenile salmonids on tidal waters, but did eat them on the freshwater reaches of streams studied. Typically, broods inhabited only the freshwater reaches of their natal stream while young, but spent progressively more time foraging on tidal waters as they grew older. The biomass of broods (and hence potential consumption) on fresh water was estimated by reconstructing the history of individual broods from census data. These results suggest that merganser broods consumed on the order of 82 000 – 131 000 coho salmon (*Oncorhynchus kisutch*) fry in the Big Qualicum River between June 10 and August 25. This is equivalent to 24–65% of the observed wild smolt production from this system, assuming that these fry would otherwise have survived as well as uneaten fry.

L'auteur a étudié, de 1980 à 1982, la prédation par les jeunes du grand bec-scie (*Mergus merganser*) des salmonidés juvéniles de trois cours d'eau du versant est de l'île Vancouver. La consommation quotidienne de poissons des jeunes becs-scies a été estimée dans la gamme allant de 80 % du poids corporel, chez les jeunes becs-scies âgés de 10 jours, à 40 % du poids corporel chez ceux âgés de 40 jours. Les jeunes becs-scies n'ont jamais été observés en train de consommer des salmonidés juvéniles dans les eaux soumises aux marées mais ils en consommaient dans les parties d'eaux douces des cours d'eau. De façon typique, les jeunes oiseaux se trouvaient dans les parties d'eaux douces de leur cours d'eau natal et passaient ensuite de plus en plus de temps à se nourrir dans les eaux soumises aux marées, à mesure qu'ils devenaient plus âgés. La biomasse des jeunes, donc la consommation potentielle, se trouvant dans les zones à eaux douces a été estimée à partir du devenir de couvées individuelles déterminé à l'aide de données d'inventaire. Les résultats obtenus portent à croire que les jeunes becs-scies ont consommé de l'ordre de 82 000 à 131 000 alevins de saumon coho (*Oncorhynchus kisutch*) dans la rivière Big Qualicum entre le 10 juin et le 25 août. Cette valeur correspond à 24–65 % de la production de tacons sauvages notée pour ce cours d'eau si l'on suppose que ces alevins auraient survécu s'ils n'avaient pas été consommées.

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Common mergansers (*Mergus merganser*) are important predators of salmon and trout populations wherever they occur in concentration on wintering grounds or raise broods during the summer months (e.g. White 1936, 1957; Beach 1937; Salyer and Lagler 1940; Elson 1950, 1962). The most convincing evidence that common mergansers limit salmon production comes from two studies on Atlantic streams: Atlantic salmon (*Salmo salar*) smolt production was doubled following just 1 yr of merganser and kingfisher control on Forest Glen Brook, Nova Scotia (White 1939; Huntsman 1941). Even greater increases were anticipated from longer-term control experiments because Atlantic salmon are vulnerable to merganser predation in fresh water for typically 2 and often 3 yr. However, the Forest Glen experiment was discontinued because it was not possible to control for differences in spawning escapement over consecutive years.

A second, more intensive study was undertaken on a 16-km section of the Pollett River in New Brunswick (Elson 1950, 1962). In this experiment, weirs were constructed to prevent natural spawning runs and known densities of Atlantic salmon fry were planted from hatcheries over a 9-yr period. Merganser control began in the sixth year of the study after monitoring salmon survival over the previous 5 yr. All predation by broods and 80% of predation by adults was eliminated. Salmon survival to smolting was 300–500% greater during the next 4 yr while the outplanted parr were protected from merganser predation; other fishes also increased in abundance. Prior to the control program, the most intense predation had been due to merganser broods. Elson (1962) estimated that predation by merganser broods during June–September was equivalent to

that by adult mergansers throughout the remainder of the year.

The fry of three species of Pacific salmon (chinook, *Oncorhynchus tshawytscha*; coho, *O. kisutch*; and sockeye, *O. nerka*) also inhabit freshwater rearing areas for up to 3 yr (typically 1 yr) before migrating to sea as smolts. Because these rearing periods are generally shorter than for Atlantic salmon, the impact of predation is expected to be less severe. Nevertheless, broods of the common merganser are sufficiently abundant on Vancouver Island streams to cause high mortality on stream-resident juvenile salmonids (Wood 1986). There is also evidence that merganser broods are more abundant on streams where salmon populations have been enhanced by hatchery and spawning channel facilities (Wood 1986).

My purpose, in this paper, is to demonstrate the potential for predation of wild salmonid stocks by common merganser broods on the coastal streams of eastern Vancouver Island. I estimate mortality of stream-resident juvenile salmon due to merganser broods based on observations of the distribution, biomass, and foraging activity of broods between late May and late August.

Study Area

Mergansers and their broods were censused on eight streams on the east coast of Vancouver Island during 1980–82 (Wood 1986); data for the four largest rivers are presented here (see Wood 1987, fig. 1). The Big Qualicum (BQ), Little Qualicum (LQ), and Englishman (ENG) rivers are comparable in size but differ greatly with respect to salmonid production (Wood 1986, table 1). Hatcheries and spawning channels are operated on both BQ and LQ. The fourth system, Quinsam – Lower Campbell (Q–LC), is much larger in terms of drainage area and discharge; it supports a large wild salmonid population which is augmented by fish released from the Quinsam River hatchery.

Methods

Estimating Biomass of Merganser Broods

Juvenile mergansers ate very few salmonids in tidal waters near the outlet of the study streams (see Results). Therefore, it was necessary to estimate the collective biomass of broods on fresh water over the rearing season. Census procedures are described in detail in Wood (1986). Brood biomass was estimated from the number and age of merganser ducklings observed on fresh water during censuses, in conjunction with published growth curves for ducklings (Erskine 1971). However, not all broods known to exist were sighted on every census, so the observed numbers and biomass underestimate the potential consumption by merganser broods.

I estimated the actual biomass on fresh water by reconstructing the history of individual broods. Broods overlooked during a census were assumed to have been upstream of the census area or hiding on fresh water if last seen on fresh water, or on tidal waters if last seen there. The number of ducklings in undetected broods was assumed to be equal to the number recorded at next sighting. These conventions provided conservative estimates of biomass on fresh water for two reasons: first, undetected broods were most likely to have been on fresh water where it is comparatively easy to hide from observers; and second, often, the number of ducklings in undetected broods would have been larger than recorded at next sighting due to mortality between censuses. Reconstructed biomass estimates for each day during the rearing period were obtained by interpolation between censuses.

Estimating Daily Consumption by Broods

Daily food consumption by juvenile mergansers was estimated from the frequency, duration, and success of foraging bouts of at least five different broods observed at the mouth of LQ. Small sculpins (primarily 0+ age class staghorn sculpins, *Leptocottus armatus*) were plentiful at this site and constituted most of the ration of the broods observed. Sculpin density was assumed to be constant over the periods of observation: June 10–12, 17, 19, and 24–26, 1981. Prey were swallowed at the surface and feeding success was evaluated without difficulty from a raised blind approximately 50 m distant using 12× binoculars. The duration and success of foraging bouts by broods were monitored for a total of 139 min (equivalent to 900 duckling-minutes). In addition, the position and activity of each brood on the estuary were recorded at 20-min intervals over a total of 38.4 h. All broods could be identified readily by the age and number of ducklings; age ranged from 10 to 35 d and number per brood from 1 to 15. Data on capture rate and the proportion of time spent foraging were used to compute daily ration of the smallest duckling. Daily consumption was estimated for other age groups by interpolation between this figure and estimates for fully fledged immature birds (see Results). To determine potential consumption, I considered predation by young ducklings (<3 wk old) and older ducklings (3–7 wk old) separately. I assumed that daily consumption was 60 and 40% of body weight for young and old ducklings, respectively, based on the interpolated estimates already described.

Estimating Salmonid Mortality

To estimate mortality of salmonids due to merganser broods, I assumed that salmonid fry were eaten only by ducklings foraging on fresh water and that coho salmon fry were the predominant salmonid species taken. The potential consumption (PC) of broods on fresh water over the rearing period, in numbers of coho fry, was computed by

$$(1)\quad \mathrm{PC} = \sum_i C_i \sum_j \frac{\bar{B}_{ij} d_j}{\bar{w}_j}$$

where $\bar{B}_{ij}$ is the average biomass of broods of age group i in time period j, $\bar{w}_j$ is the average weight of coho fry, d_j is the duration (in days) of time period j, and C_i is the daily consumption for age group i. This approximation seems reasonable in view of the uncertainty regarding age-specific daily consumption rates by ducklings and the average weight of coho fry consumed. Values of C_i, $\bar{w}_j$, and d_j are summarized in Table 1; the $\bar{w}_j$ are for streams producing smolt comparable in size with those from BQ (Paine et al. 1975). The second time period begins on June 10, since 99% of coho fry migrating downstream as fry (age 0+) had left by this date, and it is assumed that the remaining fry would contribute directly to smolt production in the following spring. The values of $\bar{B}_{ij}$ are summarized in Table 2.

To compute actual consumption, it was necessary to specify the proportion of coho fry in the diet, D. I have used a value of 50% (by weight) as an example, since I believe this to be reasonable. It was also necessary to consider the expectation of

TABLE 1. Parameter values used to compute potential consumption in equation (1).

Parameter	Description	Index	Value
C_i	Daily food consumption per duckling (as proportion of body weight) by age group i	Age <3 wk, C_1	0.6
		Age 3–7 wk, C_2	0.4
$\bar{w}_j$	Average weight of coho salmon fry (g) in time period j	May 19–June 9, $\bar{w}_1$	0.8
		June 10–30, $\bar{w}_2$	1.3
		July 1–31, $\bar{w}_3$	1.6
		August 1–25, $\bar{w}_4$	1.8
d_j	Number of days in time period j	May 19–June 9, d_1	22
		June 10–30, d_2	21
		July 1–31, d_3	31
		August 1–25, d_4	25

TABLE 2. Average reconstructed biomass of merganser ducklings and potential consumption by merganser ducklings on fresh water by age group and time period.

River	Year	Time period	Cumulative coho fry emigration[a]	Average reconstructed biomass (kg) on fresh water each day		Estimated potential consumption (PC) (in thousands of coho fry equivalents)		
				Young ducklings[b]	Old ducklings[c]	Young ducklings	Old ducklings	Total
BQ	1980	1	0.81	2.0	0	35	0	35[d]
		2	0.99	2.2	0.5			
		3	1.00	4.6	8.0	73	90	163[e]
		4	1.00	0	4.4			
	1981	1	0.98	1.3	0	22	0	22
		2	0.99	5.9	3.2			
		3	1.00	2.4	11.1	98	133	231
		4	1.00	1.8	4.9			
	1982	1	0.90	0.5	0	9	0	9
		2	0.95	4.0	0.9			
		3	1.00	4.6	10.7	99	162	261
		4	1.00	1.1	13.3			
LQ	1980	1	—	1.2	0	21	0	21
		2	—	3.2	2.1			
		3	—	0.3	6.0	34	61	95
		4	—	0.2	0.2			
	1981	1	—	4.4	0.3	76	3	79
		2	—	4.1	8.3			
		3	—	0.4	10.5	42	140	182
		4	—	0	1.2			
ENG	1981	1	—	2.0	0	35	0	35
		2	—	3.4	5.4			
		3	—	0.9	9.7	40	120	160
		4	—	0.3	2.0			
	1982	1	—	0.6	0	10	0	10
		2	—	3.3	0			
		3	—	1.0	2.0	42	19	61
		4	—	<0.1	0.6			

[a]Proportion of total coho fry downstream migration completed at begining of time period; remaining fry are assumed to contribute to smolt migration the following spring.
[b]<3 wk old.
[c]3–7 wk old.
[d]Time period 1.
[e]Time periods 2–4.

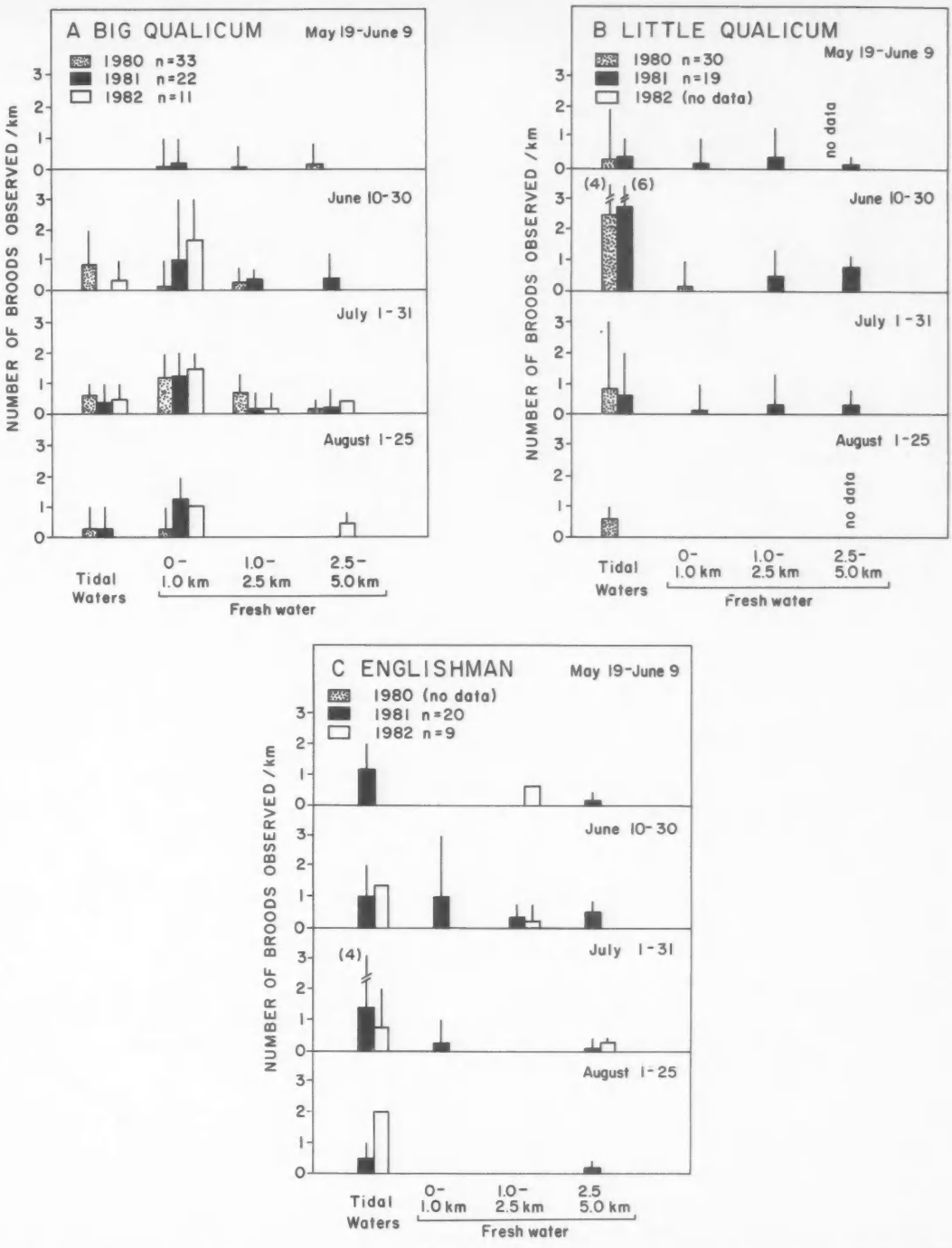

FIG. 1. Distribution of merganser broods (<50 d old) on tidal waters and freshwater reaches of the (A) Big Qualicum, (B) Little Qualicum, and (C) Englishman rivers. Time periods are those used to compute average biomass in Table 2. Histograms indicate the average and vertical bars the maximum number of broods observed per kilometre (on fresh water); counts on tidal waters include the entire estuary visible from the river mouth (about 1-km radius). The sample size, *n*, refers to the number of censuses between May 19 and August 25 each year; in 1980, the freshwater zones 1.0–2.5 and 2.5–5.0 km above the river mouth on LQ (Fig. 1B) were censused only 17 and 6 times, respectively.

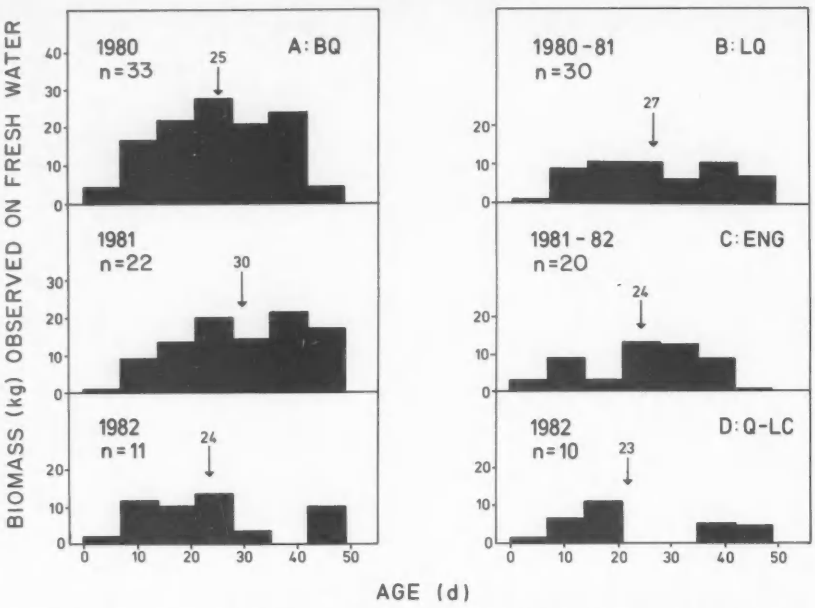

FIG. 2. Biomass–age frequency distributions of merganser broods observed on fresh water. (A) Big Qualicum, 1980–82; (B) Little Qualicum, 1980–81; (C) Englishman, 1981–82; (D) Quinsam – Lower Campbell system, 1982. Arrows indicate means; *n* refers to number of census days during May 19 – August 25.

overwinter survival so that predation of fry could be expressed in terms of smolt production. Estimates of survival rate from July to April in three Oregon streams average 19% (Chapman 1965); survival rates over the same period in Carnation Creek, Vancouver Island, averaged 24% (17–35%, 95% C.I.) from 1970 to 1981 (Holtby and Hartman 1982). If survival rate, *s*, is independent of density, consumption by broods can be estimated in coho "smolt-equivalents" by

(2) Estimated consumption = $sD(PC)$.

Results

Location of Foraging Activity

Merganser broods foraged throughout the freshwater and tidal zones of all the streams studied. However, greater concentrations were observed on the lower freshwater reaches or tidal waters (Fig. 1). Merganser broods were seen more frequently on fresh water on BQ than on the neighbouring rivers. Young ducklings frequented the freshwater reaches more commonly than older ducklings; as the broods grew, they spent an increasing proportion of time on tidal waters, especially on LQ and ENG. In terms of biomass, however, those of intermediate age (25–30 d) were predominant on fresh water (Fig. 2).

Not all broods were seen during each census so that the brood densities in Fig. 1 are too low (Wood 1986). Estimated trends in the actual brood biomass on fresh water were reconstructed from the history of individual broods (see Methods). These are summarized in Fig. 3. Fluctuations in biomass toward the end of the rearing season resulted from large broods of nearly fledged juveniles moving between fresh water and tidal waters. In terms of biomass, 51–71% of brood development took place on fresh water on BQ compared with 7–45% on LQ and 13–34% on ENG. Estimates of the average (reconstructed) biomass of young and old ducklings during four time periods (approximately 3–4 wk each) are summarized in Table 2; these were computed by integrating under curves such as those in Fig. 3.

Diet

It was difficult to study predation by broods on fresh water because they moved continuously while foraging and were soon lost from sight. My observations on BQ suggest that resident juvenile salmon, particularly coho, constituted most of the diet of ducklings of all ages foraging on fresh water. This is not surprising because coho fry were also the most conspicuous prey to a human observer. Certainly, merganser ducklings have no difficulty capturing salmonid fry. A newly hatched merganser (<4 d) was able to pursue, kill, and, after some difficulty, swallow two 2-g coho fry from among 10 fry stocked in a tank approximately 2 m in diameter and 0.2 m deep. On the BQ system, I have observed a brood of 18 (approximately 40-d-old) consume 13 salmonid fry in less than 20 s. Crop and gullet contents from two juveniles approximately 45 d old, captured on fresh water on the BQ system, August 10, 1980, reveal that both birds had fed on salmonid fry; no evidence of other fish species was found.

On tidal waters, the foraging activity of broods was comparatively easy to monitor. Small sculpins and flatfish (Bothidae or Pleuronectidae) were the most frequently consumed prey on the LQ estuary during my observations there during June 10–26, 1981. Juvenile mergansers (<50 d) were never observed to feed on salmonids during this time..

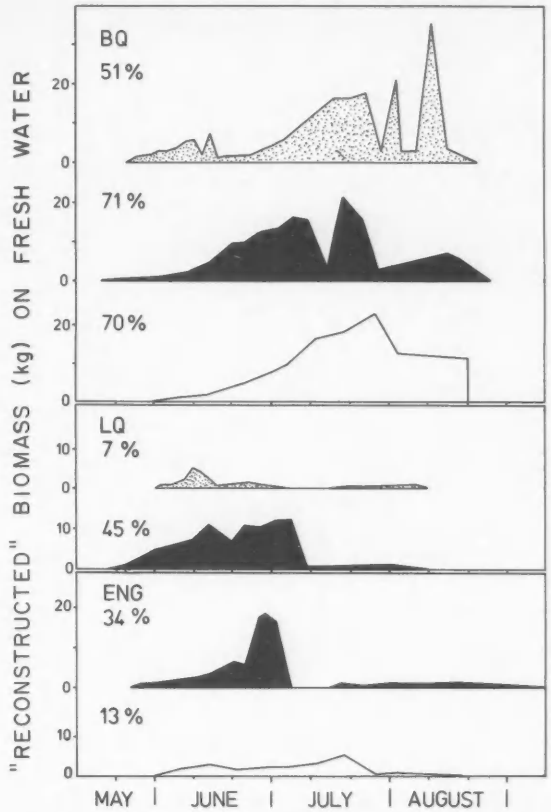

FIG. 3. "Reconstructed" biomass estimates for merganser broods <50 d old on freshwater reaches of Big Qualicum, Little Qualicum, and Englishman rivers, 1980–82. Census coverage was to 5 km upstream of river mouth. Stipple, 1980; black, 1981; white, 1982. Fluctuations are due to movements of large, nearly fledged broods moving between fresh and tidal waters. Percentage figures refer to proportion of total estimated biomass reared on fresh water.

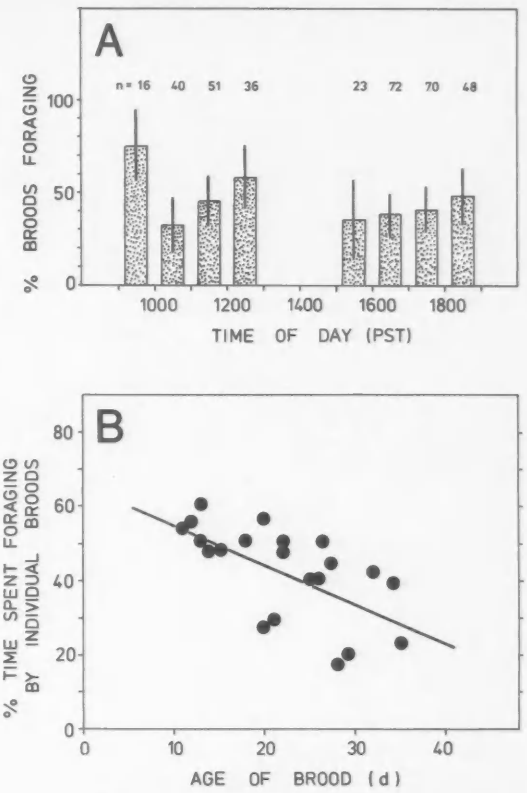

FIG. 4. Foraging activity of merganser broods on the Little Qualicum estuary with respect to (A) time of day and (B) age of brood. In Fig. 4A, n = the number of broods observed and vertical bars indicate 95% C.I. The regression in Fig. 4B is linear for arcsine-transformed data: $y = 54.1 - 0.628x$, $n = 21$, $r = -0.62$, $F_{1,19} = 11.8$, $p < 0.005$.

Estimated Consumption of Coho Salmon Fry

Broods foraged throughout the observation periods from 09:30 to 12:30 and from 15:30 to 18:30 PST (Fig. 4A). The proportion of time spent foraging declined with age for broods 10–35 d ($p < 0.005$, F-test, Fig. 4B). However, capture rate for small sculpins was not correlated with age ($p > 0.25$, t-test) or brood size (Wood and Hand 1985). On average, juvenile mergansers foraging at the mouth of LQ consumed 0.29 ± 0.01 (95% C.I.) young-of-the-year sculpins per minute. Assuming an average weight of 1.5 g/fish (derived from length distributions (Mace 1983) and a length–weight relationship (Mason and Machidori 1976)), the average rate of consumption while foraging was 0.4 g/min. Although small (<20 d) and large ducklings were equally successful at catching small sculpins, the older ducklings were able to supplement their diet with prey items too large for the young birds. Consequently, estimates of daily consumption based on the average capture rate of small sculpins, while foraging, multiplied by the proportion of time spent foraging during 12 h of daylight will underestimate the appetite of larger juveniles. I assume that this estimate is representative of ducklings at 10 d of age and have calculated consumption by older juveniles by interpolating between this estimate and the average daily appetite reported for fully fledged, immature birds held in captivity (White 1957; Latta and Sharkey 1966). The interpolated estimates of daily consumption range from greater than 80% of body weight for ducklings at 10 d of age to 40% of body weight at 40 d of age (Fig. 5). The interpolated curve becomes nonlinear when daily consumption is expressed as a proportion of body weight.

Estimates of Mortality

Estimates of consumption of coho fry by merganser broods feeding on fresh water are given in Table 3 for a diet of 50% coho fry ($D = 0.5$, as an example) and subsequent survival rates, s, ranging from 0.17 to 0.35. To calculate these estimates, I have deliberately used conservative estimates of daily consumption, C_i, of 60 and 40% of body weight for young and old ducklings, respectively. Moreover, I have ignored consumption prior to June 10, since predation then may merely remove fry that would have migrated downstream anyway. Under these assumptions, estimated consumption by broods on

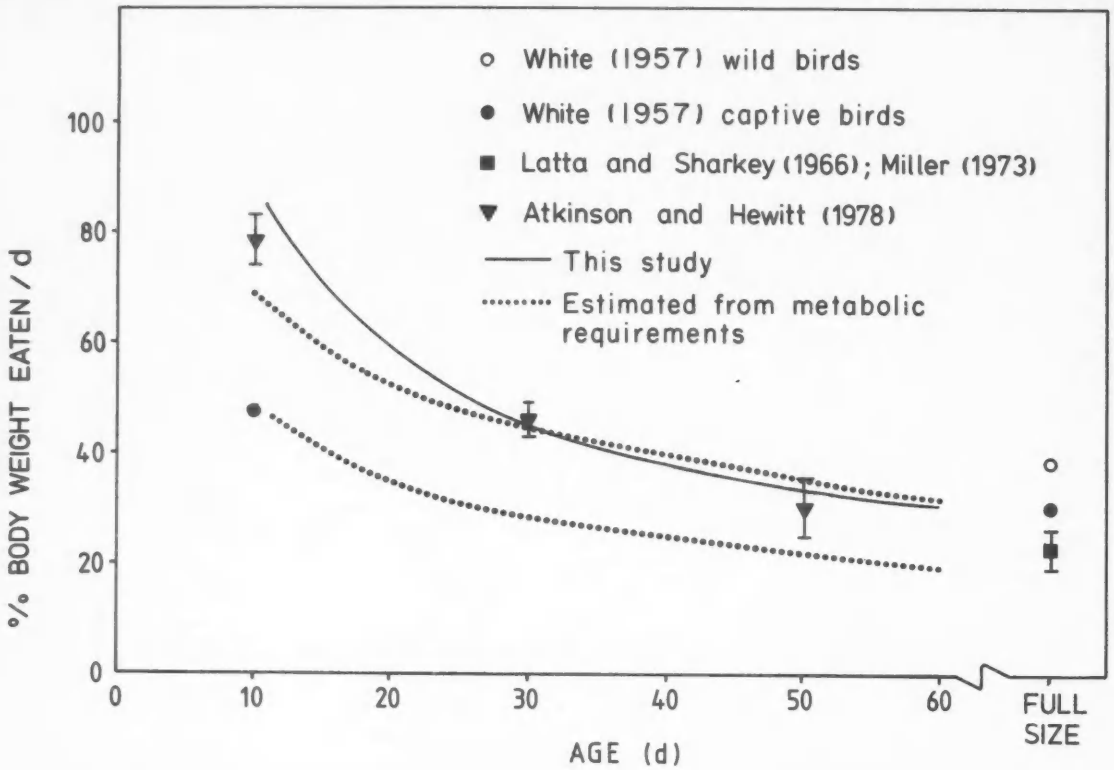

FIG. 5. Daily consumption by merganser ducklings with respect to age. The solid line was obtained by interpolating between estimates using observed capture rates of age 0+ sculpins by 11-d-old ducklings and reported estimates for fully fledged, immature birds. The interpolated line is linear when consumption is expressed in weight rather than the proportion of body weight. Dotted lines indicate upper and lower "bounds" from bioenergetic calculations. Vertical bars on point estimates are ranges for means over 2 yr (▼) or for males vs. females (■).

TABLE 3. Estimates of predation of coho fry by merganser broods on fresh water, June 10 – August 25.

River	Year	Number of smolt-equivalents eaten (thousands)		Observed wild smolt production (thousands)	Estimated consumption (as % of observed smolt production)[c]
		s = 0.2[a]	s = 0.17–0.35[b]		
BQ	1980	16	14–29	51.2	27–57
	1981	24	20–42	85.0	24–49
	1982	26	22–46	71.3	31–65
LQ	1980	10	8–17	—	—
	1981	18	15–32	—	—
ENG	1981	16	14–28	—	—
	1982	6	5–11	—	—

[a]Mean estimate from Chapman (1965).
[b]95% C.I. from Holtby and Hartman (1982).
[c]Based on range for s.

the BQ system ranges from 24 to 65% of realized coho smolt production; similarly, the estimated mortality due to merganser broods would be 19–39% of the potential smolt production (i.e. both eaten and uneaten fish). Wild smolt migrations are not enumerated on either LQ or ENG so that (percentage) mortality cannot be estimated.

Discussion

In calculating mortality due to merganser broods, I have attempted to underestimate, rather than overestimate, rates of predation. It is very unlikely that estimates of the biomass of broods on fresh water exceed the true values, since conservative procedures were used in the computations (see Methods). The greatest uncertainty arises in estimating the diet and daily consumption of merganser ducklings and the prospects for survival of uneaten fish during the remainder of the freshwater rearing period. Each of these assumptions warrants further consideration.

Stomach contents have been analyzed from over 4000 juvenile and adult mergansers foraging in a variety of habitats (White 1936, 1937, 1957; Munro and Clemens 1936, 1937; Leonard and Shetter 1936; Lindroth 1955; Mills 1962; Timken and Anderson 1969; Miller 1973; Alexander 1979; Wood 1987). Virtually all these studies indicate that mergansers eat whatever fish are abundant; on productive salmonid-rearing waters, juvenile salmonids tend to be selected over other fish species (Salyer and Lagler 1940; Lindroth 1955; Elson 1962; Alexander 1979; Anderson et al. 1985). Brown trout (*Salmo trutta*) and creek chub (*Semotilus atromaculatus*) were eaten more frequently by captive juvenile mergansers than mottled sculpins (*Cottus bairdi*) of similar size (Latta and Sharkey 1966).

Information on the diet of merganser ducklings is less extensive but is still convincing. All 20 merganser ducklings, up to one-half grown, captured on the Margaree and Cheticamp river systems, Cape Breton Island, contained salmonids but no other fishes (White 1936, 1937). Salmon and trout are the dominant fish species in these rivers. Fish remains in stomachs from 118 ducklings shot on six New Brunswick streams which support a diverse freshwater fish fauna were classified as 62% minnows (Cyprinidae), 30% salmonids, and 7% suckers (Catostomidae). Insects contributed less than 50% by volume, on average, to the diet of newly hatched ducklings <110 g and were not common in the stomachs of the older ducklings (White 1957). Cyprinids are generally absent from Vancouver Island streams (Scott and Crossman 1973), and except for sculpins, salmonids predominate in the streams I have studied. Accordingly, there is no evidence to suggest that juvenile salmonids would comprise <30% of the diet of young mergansers on these streams. In fact, the data from Cape Breton Island where salmonids predominated, and my own observations on BQ, suggest that salmonids constitute the majority of the diet by weight. If this is true, estimates of mortality based on 50% representation in the diet, by weight, will err on the low side. No doubt, sculpins and aquatic insects are also eaten by broods on fresh water (Munro and Clemens 1937), but the importance of salmonid fry in the diet should not be underestimated wherever fry are abundant (Lindroth 1955; Elson 1962; Alexander 1979).

Daily consumption by young mergansers can be estimated in three ways: first, by considering the proportion of time spent foraging and the average rate of ingestion while foraging; second, by calculating energy requirements from information about growth and metabolic rates; and finally, by monitoring the consumption of juveniles raised in captivity.

My estimate of time spent foraging is based on observations between 09:30 and 18:30 which were extrapolated to a typical 12-h day. This estimate may be biased if foraging activity differs early in the morning or in the evening. However, Foreman (1976) also reported that 45% of broods censused on rivers in northern California were foraging (excluding those fleeing when first sighted), which is in agreement with the mean (44%) of my observations presented in Fig. 4A. I assumed that the daily consumption of small sculpins by broods foraging on tidal waters would be comparable with that of small salmonids for merganser broods foraging on fresh water. This seems reasonable but has not been substantiated. I am not aware of any other data regarding typical rates of ingestion by merganser ducklings while foraging in the wild.

Basal metabolic rate (BMR) for nonpasserine birds is a power function of body weight: $M = 78.3W^{0.724}$ where M = kilocalories per 24 h and W is body weight in kilograms (Lasiewski and Dawson 1967). Young mergansers at the mean age (27 d) for the biomass–age distribution on fresh water (Fig. 2) weigh about 450 g. Accordingly, their BMR would be approximately 44 kcal/24 h. If 45% of the daylight period (12–16 h) were spent actively foraging, and another 25% swimming and preening (Foreman 1976 and pers. obs.) at an energy expenditure averaging three to five times BMR (as reported for crows (*Corvus corone*), Yom-Tov 1974), and the remaining time were passed inactively at BMR, the overall metabolic rate would be on the order of 75–130 kcal/24 h. At this age, mergansers increase in weight by roughly 20 g/d (Erskine 1971), which corresponds to an additional caloric requirement (at 1.25 kcal/g, Yom-Tov 1974) of 25 kcal/24 h. Hence, the total daily caloric requirement, assuming 80% assimilation efficiency (King and Farner 1961), would be 125–190 kcal. Since freshly killed salmon fry yield 0.91 kcal/g (Brett 1973, after subtracting energy lost to specific dynamic activity: 30% for proteins and 10% for lipids, Harper 1971), daily consumption by 4-wk-old mergansers should be at least 140–210 g or 31–47% of body weight. Although this procedure provides only a gross approximation, it does show that a daily consumption of 50% of body weight at 27 d of age is not unrealistic from bioenergetic considerations.

Additional support comes from fish consumption by young mergansers in captivity. Four merganser ducklings captured at 160 g (about 10 d old) consumed, on average, 47% of their body weight in fish over the next 3 d (White 1957). This is considerably less than my estimate for the same age; it is possible that these captive birds did not feed to satiation in the first few days after capture. In contrast, red-breasted mergansers, hatched and reared in captivity, consumed 74–83% of body weight/d during their first 20 d, 43–49% of body weight/d from 21 to 40 d of age, and 25–35% of body weight/d from 41 to 60 d (from data in Atkinson and Hewitt 1978). Daily fish consumption by another tame, but noncaptive common merganser (1150 g) averaged 38.5% of its body weight (White 1957). These data are also summarized in Fig. 5 to permit comparison with the curve I have derived from observations of wild birds. The derived curve may overestimate consumption by very young birds although activity, and hence appetite, is likely to be higher among wild birds than those retained in cages. Bounds from bioenergetic calculations (as described above) are also plotted against age in Fig. 5. The estimates of 60 and 40% of body weight for young (<3 wk) and old (3–7 wk) ducklings are supported by all the alternative data. If, in fact, young ducklings in the wild consume >60% of their body weight/d, overall consumption by broods will have been underestimated.

It is evident from the preceding discussion that predation by merganser broods must be regarded as a significant source of mortality among stream-resident juvenile salmon in the BQ

system. Yet, following a survey of streams throughout British Columbia, Munro and Clemens (1937) concluded that predation by mergansers was not a serious problem for Pacific salmon populations. I do not dispute their conclusion with regard to predation of seaward migrants (Wood 1987); however, their estimates of merganser brood density are extremely low in comparison with my estimates. While it is conceivable that nesting densities have increased over the past 45 yr, it seems more likely that their census was inadequate. Sampling curves presented by Wood (1986) indicate that a river must be censused frequently (at least once a week) to obtain reliable estimates of merganser brood density. Also, in analyzing stomach samples, Munro and Clemens did not distinguish between predation on fresh water where salmonids predominate in the diet and predation in tidal waters where other prey are taken. If most of their specimens were collected on tidal waters (where mergansers are most conspicuous and least wary), the incidence of salmon in stomachs would have been underestimated. Elson (1962) also expressed doubts about Munro and Clemens' conclusion with regard to the impact of mergansers on stream-resident salmonids in the Cowichan River system, situated about 80 km southeast of ENG.

The potential for predation by merganser broods was considerably higher on BQ than on either LQ or ENG. In part, this was due to higher brood densities on the former stream, possibly because breeding pairs aggregate there in response to enhanced fry and smolt migrations during March–May (Wood 1986). But also, within the BQ system, a greater proportion of broods are found on fresh water as opposed to tidal waters. The BQ estuary is small in comparison with those of LQ and ENG, so that high freshwater densities on BQ may reflect a scarcity of alternative prey for the ducklings. If this is true, then mortality on wild salmonids in BQ might be unusually intense as a consequence of the combined effect of high nesting density and scarcity of nonsalmonid prey species. Alternatively, broods may forage more intensively on fresh water on the BQ system because wild salmonids are more abundant there than at either LQ or ENG. (Unfortunately, wild smolt migrations are not enumerated regularly in the latter streams.) In this case, (percentage) mortality on BQ would be representative of other streams.

It is not clear whether mortality due to merganser broods has any effect on the eventual size of smolt migrations in Vancouver Island streams. Because merganser ducklings kill salmonid fry during the summer months, there is ample opportunity (30–40 wk) for compensation to occur if overwintering survival is further limited by food or habitat (e.g. Chapman 1965). Subsequent mortality appears to depend largely on the minimum rearing area during periods of low flow (Marshall and Britton 1980) and physical displacement during freshets (e.g. Scrivener and Andersen 1982). Because the risk of physical displacement during freshet depends on the availability of cover (Tschaplinski and Hartman 1982), and the risk of behavioural displacement during low flow depends on availability of suitable rearing territory (Chapman 1962; Hartman 1965), mortality in both cases will be determined by the number of "surplus" individuals and will, therefore, be compensatory. Provided merganser broods remove only surplus individuals, their predation may have little consequence for subsequent smolt production.

Merganser-control programs on Atlantic streams have apparently been successful at increasing salmon smolt production (Elson 1962; Anderson et al. 1985), but there are important differences between the Atlantic and Pacific situations. Atlantic salmon remain in fresh water for 2–3 yr (as do steelhead trout, *Salmo gairdneri*, in Pacific streams); even if mortality during the first winter reduced resident populations below the level determined by brood predation, additional predation during the next summer would diminish the cohort still further. Also, freshet mortality is probably higher in Pacific than Atlantic streams. Finally, conclusions about mortality in Elson's (1962) study were based on hatchery fry outplanted at higher densities than occurred naturally. Higher than average mortality would be expected in this situation because mergansers congregate in favourable feeding areas (Wood 1985a, 1985b). For these reasons, it seems unlikely that merganser broods could limit the freshwater production of Pacific salmon (excluding steelhead trout) to the same extent that they appear to limit survival of Atlantic salmon in some rivers. Nevertheless, merganser broods have the potential to exert substantial mortality on Pacific salmon resident in streams such as BQ, and further investigation is warranted.

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Phosphorus Species in the Surficial Sediments of Lakes of Eastern North America

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Ostrofsky, M. L. 1987. Phosphorus species in the surficial sediments of lakes of eastern North America. Can. J. Fish. Aquat. Sci. 44: 960–966.

Species of phosphorus, total iron, and organic matter were determined from surficial profundal sediments of 66 lakes of eastern North America. The lakes represented a broad range of lake type, from oligotrophic to eutrophic and from soft water to moderately alkaline. The sediment characteristics were less variable than the lake characteristics. Highly significant correlations were found between percent loss on ignition and sedimentary organic phosphorus and between sedimentary iron and NH_4Cl-extractable, NaOH-extractable, HCl-extractable, total inorganic, and total phosphorus in the sediments. There was no relationship between spring total phosphorus or alkalinity and any sediment character measured. The results suggest that lakes with high sedimentary iron have disproportionately higher concentrations of NH_4Cl and NaOH-extractable phosphorus, two species that are most likely to contribute to internal loading of phosphorus.

On a déterminé les variétés de phosphore, la teneur en fer total et la quantité de matières organiques contenues dans les sédiments superficiels recueillis au fond de 66 lacs de l'est de l'Amérique du Nord. Ceux-ci représentent un vaste écart de types de lacs, allant de lacs oligotrophes à des lacs eutrophes et de lacs d'eau douce à des lacs modérément alcalins. Les caractéristiques des sédiments étaient moins variables que les caractéristiques des lacs. Il existe des corrélations nettement significatives entre la perte en pourcentage à l'ignition et le phosphore organique sédimentaire, et entre, d'une part, le fer sédimentaire et, d'autre part, le phosphore total inorganique et le phosphore total extractibles par NH_4Cl, NaOH et HCl contenus dans les sédiments. Il n'y a pas de relation entre, d'une part, le phosphore total printanier ou l'alcalinité et, d'autre part, toute caractéristique sédimentaire quantifiée. Les résultats portent à croire que les lacs à teneur élevée en fer sédimentaire contiennent de plus fortes concentrations disproportionnées de phosphore extractible par NH_4Cl et NaOH, soit deux espèces qui ont le plus tendance à contribuer à la charge interne de phosphore.

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A large fraction of the annual phosphorus load to lakes is retained by the lake sediments. This sedimented phosphorus can, under appropriate circumstances, be released as biologically available phosphorus, and recent studies have shown lake sediments to be a significant source of phosphorus in the phosphorus economy of many lakes (Nürnberg and Peters 1984). As a result, limnologists have become more interested in the quality and quantity of sediment phosphorus. The existing paradigm for "internal" phosphorus loading to lakes involves redox-mediated release of phosphorus bound to iron. While limnologists have available a number of models which help make predictions about anoxia, and therefore redox status, in the hypolimnia of lakes, very little is known about what determines the quantity of iron-bound or other phosphorus species in the sediments of any lake. Although temperature, bioturbation, physical mixing, etc., have all been shown to have an effect on phosphorus release rates, the chemical species of phosphorus present in the sediments almost certainly are among the more important factors regulating release.

Sediment phosphorus species have been analysed previously, although the amount or kinds of phosphorus were only seldom compared with other sediment or lake characteristics. A notable exception is the work of Williams et al. (1976), where correlations were found between sediment characteristics and phosphorus species for 48 surficial sediment samples taken throughout Lake Erie. Phosphorus species, iron, manganese, organic matter, mean grain size, and percent sand, silt, and clay were all highly intercorrelated. Although the sediments of large lakes such as Lake Erie are highly heterogeneous, these interrelationships suggest that the quality and quantity of phosphorus in these sediments may be predicted from knowledge of only a few variables.

It is unknown if these correlations exist in other lakes or are unique to each lake or group of lakes sharing similar basin geology and hydrologic characteristics. The purpose of this study was to examine the profundal sediments of a variety of lakes from eastern North America and to look for significant correlations between species of phosphorus and other lake and sediment characteristics. It was hoped that any significant correlations found might serve as the basis for empirical models enabling limnologists and lake managers to predict sediment phosphorus species and, ultimately, potential rates of internal phosphorus loading.

Methods

Lakes were chosen for easy accessibility and readily avail-

TABLE 1. Characteristics of the lakes sampled.

Region and lake	Area (ha)	A_d/A_0	Spring [TP] ($\mu g \cdot L^{-1}$)	Alkalinity ($meq \cdot L^{-1}$)	Depth (m)	Temperature of surface sediments (°C)
Ontario						
Algonquin Park						
Kearney	32	54	12	0.10	10.5	6
Costello	34	35	10	0.11	15	6
Brewer	41	11	9	0.12	11	6
Clarke	20	168	10	0.19	11	6
Little McCauley	18	14	7	0.11	10	7
Found	13	2.4	7	0.15	32	5
Haliburton						
Beech	136	379	9	0.36	21	8
Green	122	393	10	0.38	11	10
Pine	108	278	10	0.39	10	9
Cranberry	69	412	9	0.36	7	9
Connecticut						
Linsley	9	36	51	1.95	12	6
Quonnipaug	45	15	27	0.69	13	8
Black	30	10	25	1.09	6	12
Quassapaug	108	4.3	16	0.16	18	8
Taunton	51	6.7	23	0.57	9	10
Kenosia	23	56	38	1.68	5	16
Ball	36	2.6	37	1.18	14	7
Squantz	115	13	16	0.57	13	10
Bantam	366	23	26	0.79	7	17
Mt. Tom	25	11	10	0.49	14	7
Waramaug	272	13	27	0.51	11	11
West Side	17	51	14	0.95	10	8
Tyler	73	22	23	0.86	7	17
West Hill	95	3.5	9	0.17	17	7
Highland	178	10	11	0.33	16	6
East Twin	225	4.7	20	2.34	17	7
Wononscopomuc	141	4.7	44	2.53	26	6
Mudge	80	37	27	2.87	10	10
Wononpakook	66	17	43	2.60	7	12
Cream Hill	29	5.6	16	0.52	10	9
Vermont						
Dunmore	399	13	8	0.30	30	8
Shelburne	182	11	111	2.13	5	22
Iroquois	93	11	30	0.96	10	12
Fairfield	188	8.1	27	0.62	12	11
Carmi	556	5.6	23	0.78	9	20
Eden	75	13	8	0.56	11	6
Wolcott	28	14	12	0.25	6	11
Caspian	298	6.1	6	1.32	42	10
Shadow	81	18	7	0.96	41	5
Parker	97	23	16	1.32	13	9
Crystal	315	19	5	0.70	29	5
May	47	9.4	11	0.33	9	10
Echo	220	28	6	0.71	34	6
Island	246	10	6	0.39	15	9
Groton	168	29	8	0.20	11	11
Peacham	134	6.6	8	0.35	14	8
Ewell	20	40	16	2.10	16	6
Harvey's	166	13	14	1.32	40	5
Morey	218	9.5	34	0.91	12	9
Fairlee	187	28	10	0.69	14	8
Pennsylvania						
Conneaut	376	19	18	1.40	19	12
Crystal	7	7	28	1.21	7	12

TABLE 1. (*Concluded*)

Region and lake	Area (ha)	A_d/A_0	Spring [TP] ($\mu g \cdot L^{-1}$)	Alkalinity ($meq \cdot L^{-1}$)	Depth (m)	Temperature of surface sediments (°C)
Sandy	59		9	1.26	11	10
Sugar	43	142	48	1.30	5	20
Canadohta	69	29	22	0.89	12	9
Edinboro	97	43	49	1.62	10	15
LeBoeuf	31	92	25	2.28	9	8
Pleasant	26	14	19	1.65	11	8
New York						
Western New York						
Findley	120	11	14	1.61	12	10
Bear	45	57	17	1.02	7	19
Lower Cassadaga	38	35	24	1.72	15	8
Silver	302	15	31	1.79	11	20
Java	20	13	54	1.77	5	17
Lime	64	4.3	14	2.34	8	11
Adirondacks						
South	202			0.00[a]		
Big Moose	515			0.00[a]		

[a]South and Big Moose lakes are affected by acid precipitation.

able, or easily obtainable, spring phosphorus data. Phosphorus and morphometric data for six Algonquin Park lakes were taken from Scheider (1978). Data for four Haliburton lakes were from Dillon (1974). Lake characteristics of 20 Connecticut lakes were from Frink and Norvell (1984). The Vermont Department of Water Resources provided unpublished data on 20 Vermont lakes. Characteristics of six western New York lakes were from the New York Department of Environmental Conservation. Data on two Adirondack lakes were provided by J. S. Owen (SUNY-Syracuse, pers. comm.). Information on eight Pennsylvania lakes is from M. L. Ostrofsky (unpubl. data).

Sediment samples were obtained from a single location in the deepest area of the lake, or, where a bathymetric map was unavailable, from the geometric center of the lake. Samples were collected with a Wildco K.B. corer. Cores were extruded in the field, and the surface 2.5 cm of sediment was placed in polyethylene bags and held on ice until analyses could be started (always within 1 wk). Surface and bottom temperature, surface and bottom dissolved oxygen concentrations, and surface alkalinity were also measured. The depth from which the sediment was obtained was also noted. Table 1 presents descriptive data on all the lakes.

In the laboratory, species of phosphorus in the sediments were determined using the sequential extraction procedure of Hieltjes and Lijklema (1980). Sediments were extracted for 2 h twice with 1 *M* NH_4Cl (interstitial plus loosely bound plus $CaCO_3$-adsorbed phosphorus), for 17 h with 0.1 *N* NaOH (iron-plus aluminum-bound phosphorus), and 24 h with 0.5 *N* HCl (calcium-bound phosphorus). Total sedimentary phosphorus was determined following $HNO_3/HClO_4$ digestion. All phosphorus determinations were based on the heteropoly blue technique outlined in Strickland and Parsons (1968). Organic-bound phosphorus was calculated as the difference between total sedimentary phosphorus and the sum of the inorganic fractions. Sediment dry weight (24 h at 100°C), loss on ignition (2 h at 550°C), and total iron (orthophenanthroline method on $HNO_3/HClO_4$ digests, APHA 1971) were also determined on all samples. All analyses and extractions were done in triplicate. Average coefficient of variation was less than 5%. Mean values are reported here and were used for subsequent regression analyses. All data are reported on a dry weight basis.

Results and Discussion

Experimental

Mean values for sedimentary phosphorus species, iron, and loss on ignition are given in Table 2, and summary statistics for the entire collection of lakes are given in Table 3. All phosphorus species demonstrated a lognormal distribution. Organic bound phosphorus (ORG-P) was the least variable phosphorus species (coefficient of variation = 28%), and loosely sorbed phosphorus (NH_4Cl extractable) was the most variable (coefficient of variation = 198%). Most sediment variables measured were highly intercorrelated. A matrix of correlation coefficients is given in Table 4. There was a highly significant relationship between organic content of the sediments measured as percent weight loss on ignition (LOI) and organic phosphorus (Fig. 1). Remaining phosphorus fractions were highly correlated with iron. Due to the lognormal distribution of these variables, regression analyses required the use of natural log-transformed data. These relationships are shown in Fig. 2–6.

All phosphorus fractions in the sediments were highly correlated with total sediment phosphorus (TOT-P), and all inorganic phosphorus fractions are highly correlated with total inorganic phosphorus (IN-P), and to each other:

(1) $\ln(NH_4Cl\text{-}P) = 2.89 \ln(TOT\text{-}P) - 19.36 \quad r = 0.57$

(2) $\ln(NaOH\text{-}P) = 1.78 \ln(TOT\text{-}P) - 7.49 \quad r = 0.84$

(3) $\ln(HCl\text{-}P) = 0.77 \ln(TOT\text{-}P) - 0.58 \quad r = 0.44$

TABLE 2. Sediment characteristics of the 66 lakes investigated. All phosphorus species in $\mu g \cdot g$ sediment dry weight^{-1}, iron in $mg \cdot g$ sediment dry weight^{-1}, and LOI in percent of dry weight.

Region and lake	NH_4Cl-P	NaOH-P	HCl-P	TOT-P	Iron	LOI
Ontario						
Algonquin Park						
Kearney	0	656	435	2260	41.3	24.5
Costello	15	748	199	2367	21.4	31.6
Brewer	3	831	179	2413	28.6	35.4
Clarke	21	1486	547	3513	111.3	37.5
Little McCauley	0	543	75	2137	22.8	42.3
Found	52	855	165	2894	56.8	41.8
Haliburton						
Beech	9	772	737	2413	43.3	13.9
Green	1	336	609	1776	32.9	12.6
Pine	2	318	663	1760	32.4	9.6
Cranberry	0	140	432	1487	25.0	17.5
Connecticut						
Linsley	31	627	267	2721	64.7	21.3
Quonnipaug	40	1304	369	3128	71.3	22.8
Black	8	204	96	1570	33.3	50.1
Quassapaug	53	1474	253	3485	59.4	32.4
Taunton	56	640	226	3255	45.4	34.2
Kenosia	31	645	283	2765	58.4	22.2
Ball	85	1057	312	3212	55.1	35.0
Squantz	46	1290	378	3410	78.4	22.0
Bantam	27	652	264	3463	47.9	31.1
Mt. Tom	65	766	202	2746	50.8	25.5
Waramaug	135	1515	345	3564	47.6	26.9
West Side	27	705	147	2897	40.2	35.2
Tyler	18	429	154	2192	37.0	49.9
West Hill	19	697	175	2257	42.9	27.0
Highland	370	1944	373	3354	48.7	24.8
East Twin	31	300	206	2217	41.1	35.9
Wononscopomuc	10	300	309	1756	52.2	24.4
Mudge	50	403	290	2167	49.2	24.0
Wononpakook	34	323	254	2321	56.5	34.2
Cream Hill	18	423	120	2269	23.0	43.1
Vermont						
Dunmore	2	552	262	2068	60.6	14.6
Shelburne	28	237	168	2135	31.2	44.3
Iroquois	82	674	337	2894	45.3	29.9
Fairfield	73	431	446	2500	38.4	21.8
Carmi	28	233	442	2267	36.7	19.7
Eden	10	345	173	1743	43.4	19.5
Wolcott	20	671	82	2665	22.7	37.3
Caspian	326	3071	709	5784	67.1	19.2
Shadow	332	2844	452	5075	80.5	29.0
Parker	74	662	411	2486	55.9	16.5
Crystal	6	315	222	1342	38.4	17.1
May	53	323	116	1889	22.0	32.0
Echo	31	1183	429	2863	49.5	19.5
Island	38	535	150	2537	36.9	28.4
Groton	15	462	122	2306	27.6	31.9
Peacham	86	458	136	2312	26.5	29.3
Ewell	59	413	177	2646	43.2	52.0
Harvey's	872	5879	574	9212	97.2	27.8
Morey	114	277	241	2406	42.7	24.9
Fairlee	41	511	232	2310	39.0	23.1
Pennsylvania						
Conneaut	39	921	234	2326	51.8	16.8
Crystal	31	363	92	1814	36.8	54.0
Sandy	6	365	97	1900	108.0	21.0
Sugar	54	1646	275	3025	58.3	23.1

TABLE 2. (*Concluded*)

Region and lake	NH_4Cl-P	NaOH-P	HCl-P	TOT-P	Iron	LOI
Canadohta	33	773	162	2253	38.2	18.3
Edinboro	35	934	197	2358	44.6	18.9
LeBoeuf	20	753	178	1988	50.0	13.2
Pleasant	41	564	180	2113	42.4	21.2
New York						
Western New York						
Findley	80	1363	243	2953	52.0	18.7
Bear	12	449	166	1693	45.1	13.7
Lower Cassadaga	53	248	158	1347	26.1	25.0
Silver	22	378	364	1834	32.9	18.1
Java	52	929	152	2868	46.4	21.6
Lime	44	188	130	1397	22.7	23.9
Adirondacks						
South	6	413	43	1329	—	44.0
Big Moose	27	1307	331	1926	—	40.0

TABLE 3. Descriptive statistics for sediment characteristics of the 66 lakes investigated. All phosphorus species in $\mu g \cdot g$ sediment dry weight^{-1}, iron in mg·g sediment dry weight^{-1}, and LOI in percent of dry weight.

Parameter	Mean	Range	SD	Coefficient of variation
TOT-P	2580	1329–9212	1138	44
ORG-P	1428	261–2520	401	28
IN-P	1153	308–7325	1036	90
NH_4Cl-P	62	0–872	123	198
NaOH-P	819	140–5879	845	103
HCl-P	272	43–737	158	58
Iron	46.5	21.4–111.3	18.9	41
LOI	27	9.6–54	10.2	38

$$\text{(4)}\quad \ln(\text{IN-P}) = 1.49 \ln(\text{TOT-P}) - 4.77 \qquad r = 0.85$$

$$\text{(5)}\quad \ln(\text{ORG-P}) = 0.49 \ln(\text{TOT-P}) + 3.38 \qquad r = 0.48.$$

Spring total phosphorus, [TP], which has been used as a powerful predictor of such in-lake characteristics as mean chlorophyll (Dillon and Rigler 1974), Secchi transparency (Patalas 1972), and hypolimnetic oxygen deficit (Cornett and Rigler 1979), and alkalinity were not significantly correlated with any sedimentary phosphorus species. This result suggests that neither can be used to predict the sediment characteristics of these lakes. The observed intercorrelations of the phosphorus species suggest that relatively constant relationships exist among the various forms of phosphorus within the sediments regardless of a lake's trophic status or alkalinity.

The collection of lakes described here represents a broad range of lake types, from oligotrophic to eutrophic and from soft to alkaline. Nevertheless, the sediments of these lakes were quite similar in that there were constant relationships among the measured sediment characteristics. Organic sediment phosphorus was a function of sediment organic content measured as LOI (Fig. 1). Sediment organic content was correlated with the ratio of drainage basin area to lake area ($r = -0.35$, $n = 63$) rather than to spring total phosphorus, a measure of trophic status. Inorganic sediment phosphorus was highly correlated with the iron content of the sediments (Fig. 5), mostly because iron-bound phosphorus was a large

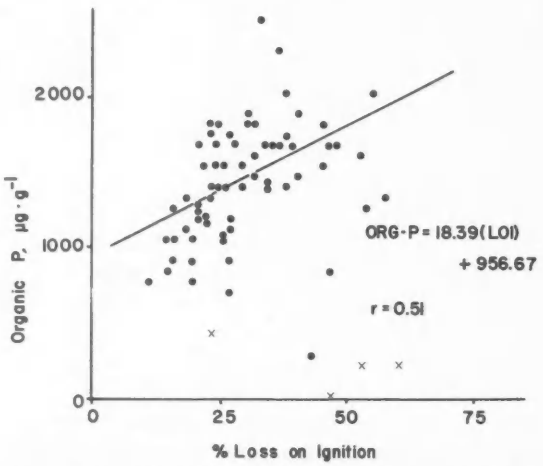

FIG. 1. Relationship ($p < 0.01$) between percent dry weight lost on ignition and sediment organic phosphorus in the 66 lakes sampled (solid circles) and in European lakes (crosses). See Table 5 for European lake data and sources.

fraction of total inorganic phosphorus, but also because other inorganic fractions are also strongly correlated with sediment iron (Fig. 2, 3, and 4). Total sediment phosphorus then was a function of LOI and iron although stepwise multiple regression analysis suggested that LOI does not significantly improve the predictive ability over that possible with iron alone (Fig. 6).

Sediments with more total phosphorus tended to have relatively more inorganic phosphorus (slope of the regression line (4) was significantly greater than 1, $p < 0.05$) and less organic phosphorus. Increased inorganic phosphorus was largely due to increased NH_4Cl-P and NaOH-P (slopes significantly greater than 1). HCl-P was a relatively constant fraction of inorganic phosphorus (slope not different from 1).

Literature

These results are in close agreement with those of Williams et al. (1976), who also found significant relationships between organic matter and organic phosphorus and between iron and

TABLE 4. Matrix of correlation coefficients among lake and sediment characteristics measured on the 66 lakes. Correlation coefficients greater than 0.24 and 0.31 are significant at $*p < 0.05$ and $**p < 0.01$, respectively.

	NaOH-P	HCl-P	IN-P	ORG-P	TOT-P	Iron	LOI	Alkalinity	[TP]
NH_4Cl-P	0.90**	0.37**	0.91**	0.15	0.88**	0.42**	−0.01	0.07	−0.09
NaOH-P	—	0.45**	0.99**	0.11	0.94**	0.58**	−0.06	−0.05	−0.13
HCl-P		—	0.56**	−0.20	0.44**	0.36**	−0.46**	−0.09	−0.14
IN-P			—	0.07	0.94**	0.57**	−0.12	−0.05	−0.14
ORG-P				—	0.42**	0.16	0.51**	0.09	0.17
TOT-P					—	0.58**	0.05	−0.02	−0.07
Iron						—	−0.15	0.12	−0.01
LOI							—	−0.04	0.14
Alkalinity								—	0.56**

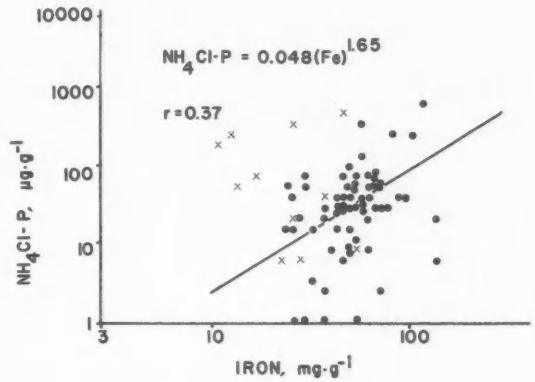

FIG. 2. Relationship ($p < 0.01$) between total sediment iron and NH_4Cl-extractable phosphorus. Symbols as in Fig. 1.

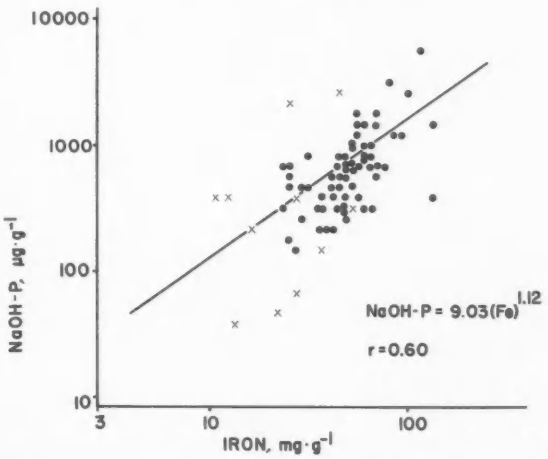

FIG. 3. Relationship ($p < 0.01$) between total sediment iron and NaOH-extractable phosphorus. Symbols as in Fig. 1.

inorganic phosphorus species in Lake Erie sediments. Direct comparison with Williams et al. (1976) is not possible because of different analytical methods used. Hieltjes and Lijklema (1980) have suggested that the CDB extraction technique used by Williams et al. (1976) can include an appreciable fraction of the calcium-bound phosphorus in the nonapatite inorganic phosphorus (NAI-P) fraction and give incomplete extraction of

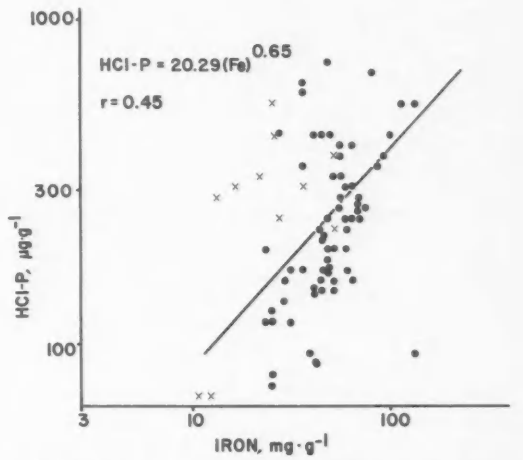

FIG. 4. Relationship ($p < 0.01$) between total sediment iron and HCl-extractable phosphorus. Symbols as in Fig. 1.

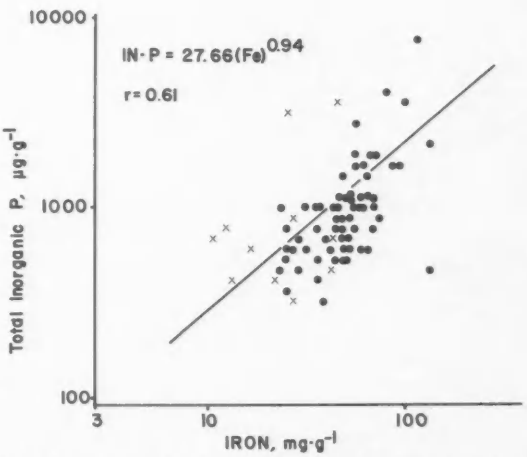

FIG. 5. Relationship ($p < 0.01$) between total sediment iron and total inorganic sediment phosphorus. Symbols as in Fig. 1.

the aluminum-bound phosphorus. Nevertheless, total phosphorus should be comparable between the two studies. When the two regression lines between iron (as a percentage of sediment weight) and total phosphorus were compared, the

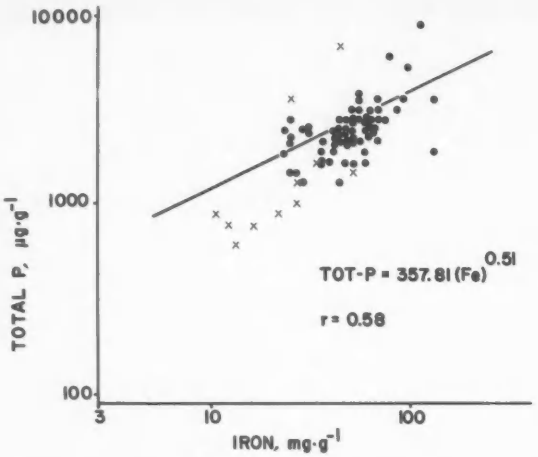

FIG. 6. Relationship ($p < 0.01$) between total sediment iron and total sediment phosphorus. Symbols as in Fig. 1.

TABLE 5. Phosphorus species, iron, and LOI from the sediments of European lakes. Data derived from Tiren and Pettersson (1985) for Swedish lakes and Lake Balaton, Klapwijk et al. (1982) for Netherlands lakes, and vanEck (1982) for Hollands Diep/Haringvliet (HD/HV). All units as in Table 2.

Region and lake	NH_4Cl-P	NaOH-P	HCl-P	TOT-P	Iron	LOI
Sweden						
Ringsjön	7	69	241	1020	25.0	—
Tåkern	6	44	342	920	20.0	—
Fysingen	9	315	385	1430	45.4	—
Östen	23	375	452	1260	23.8	—
Vallentunasjön	42	139	316	1670	32.1	—
Hungary						
Balaton	64	39	284	610	12.5	—
Netherlands						
Braassem	432	2232	540	3600	23.0	21
Westeinder	312	416	72	800	12.0	44
Reeuwijk	72	216	312	800	15.0	49
Nieuwkoop	198	414	72	900	10.0	57
HD/HV	630	2870	210	7000	40.0	—

slopes were significantly different ($p > 0.05$). Apparently, the relationship between total phosphorus and iron from all regions within Lake Erie is different from the relationship between total phosphorus and iron from the profundal zones of different lakes although different analytical methods for both phosphorus and iron may contribute somewhat to this difference.

As mentioned above, there are no other extensive data sets with which to compare these present results. A compilation of some data from European lake sediments is shown in Table 5. These data are from studies where sediment phosphorus species were determined using the Hieltjes and Lijklema (1980) technique. These data are, for the most part, within the ranges reported for the 66 North American lakes, and the individual lake data are plotted in the appropriate figures although these data were not included in the regression analyses. The European lake data are consistent with the North American data, suggesting the possibility of widespread application of the relationships developed here.

As the regression analyses indicate, iron has more of a bearing on sediment phosphorus chemistry than does trophic status or alkalinity. Lakes with more sedimentary iron tend to have disproportionately more iron-bound and loosely sorbed phosphorus, species that are most likely to contribute to internal phosphorus loading: iron-bound phosphorus is released at low redox potentials, and loosely sorbed phosphorus includes interstitial soluble reactive phosphorus which can migrate into the overlying hypolimnetic waters. Therefore, lakes most susceptible to internal loading will be those which have both iron-rich sediments and anoxic hypolimnia.

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An Analysis of Errors in Catch Projections for Canadian Atlantic Fish Stocks

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Rivard, D., and M. G. Foy. 1987. An analysis of errors in catch projections for Canadian Atlantic fish stocks. Can. J. Fish. Aquat. Sci. 44: 967–981.

Two techniques were used to identify and evaluate the components of error inherent in the catch projection method used in the assessment of Canadian Atlantic fish stocks. Firstly, a retrospective analysis was used to evaluate, for the projections made in 1979 and 1981, the impact of the actual error made in input variables such as catch-at-age, mean weight-at-age, recruitment, and stock size. Secondly, the variance of projections was estimated from the variance of input variables. From the retrospective analysis, the principal causes of error in catch projections were identified as the estimation of stock size, as well as the estimation and forecast of fishing mortalities for the projection years. The difference between actual catch and assumed catch for the first year of a 2-yr projection did not appear to be a major source of bias for catch projections. The coefficients of variation of the catch projected at $F_{0.1}$ were estimated as follows: 15–20% for the projections of Atlantic cod (*Gadus morhua*) catches; 25–50% for those of haddock (*Melanogrammus aeglefinus*); 28% for those of pollock (*Pollachius virens*); 16% for those of redfish (*Sebastes* sp.); and 35–42% for those of herring (*Clupea harengus*). The uncertainties associated with abundance estimates for prerecruited age-groups and estimates of stock size emerged as key factors in the projections. Also important was the effect of uncertainties associated with the forecast of reference fishing mortalities (partial recruitment coefficients × $F_{0.1}$) for the projection period, e.g. uncertainties resulting from changes in fish catchability, in fleet behavior, and in fishing patterns.

Deux techniques ont servi à identifier et à évaluer les composantes de l'erreur associée à la méthode de projection des captures commerciales utilisée lors de l'évaluation des stocks de poisson dans l'Atlantique canadien. En premier lieu, une étude rétrospective a permis d'évaluer, pour les projections faites en 1979 et en 1981, l'impact d'erreurs faites sur les variables d'entrée, telles la prise et le poids moyen par groupe d'âge, le recrutement et l'abondance du stock. En second lieu, la variance des prises prévues fut estimée à partir de la variance des variables d'entrée. A partir de l'étude rétrospective, l'estimation de l'abondance du stock, ainsi que l'estimation et la prédiction des taux de mortalité par pêche pour les années de projection, ont été identifiées comme les principales causes d'erreur dans les projections. La différence entre la prise actuelle et la prise utilisée pour la première année de la période de projection (qui est de 2 années) n'est pas apparue comme une cause majeure de biais pour les projections. La coefficient de variation des prises projetées à $F_{0.1}$ s'est établi comme suit : 15–20 % pour les projections de captures de morue franche (*Gadus morhua*); 25–50 % pour celles d'aiglefin (*Melanogrammus aeglefinus*); 28 % pour celles de goberge (*Pollachius virens*); 16 % pour celles de sébaste (*Sebastes* sp.); et 35–42 % pour celles de hareng (*Clupea harengus*). Les incertitudes associées à l'estimation de l'abondance des groupes d'âge pré-recrutés et à l'estimation de l'abondance du stock sont apparues comme des facteurs importants pour ces projections. Egalement important fut l'effet des incertitudes associées à la prévision des mortalités par pêche de référence (coefficients de recrutement partiel × $F_{0.1}$) pour la période couverte par les projections, e.g. les incertitudes résultant de changements de la capturabilité du poisson, du comportement de la flotte de pêche et des patrons de pêche.

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On the Canadian Atlantic coast, the management of many marine fish stocks is based on a quota system. Quotas are generally established from the determination of the total allowable catch (TAC) on a given stock. The estimation of a TAC generally involves the reconstruction of historical population levels from a virtual population analysis (Gulland 1965; Pope 1972) and a projection of future catches. For such projections, the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) and the Northwest Atlantic Fisheries Organization (NAFO) use a reference fishing mortality level called $F_{0.1}$ (i.e. the rate of fishing mortality at which the slope of the yield-per-recruit curve is 1/10 the value at zero fishing mortality). This fishing mortality level, which is lower than the fishing mortalities which were imposed on many fish stocks of the Northwest Atlantic in the early 1970s, yields in the long term certain economic benefits. As the biomass goes up due to reduced fishing effort, so do the catch rates, and as a result of this, the cost of catching fish goes down. Also, as more fish have a chance to grow to older ages, bigger, more valuable fish are produced on the average. With a lower fishing mortality, the fisheries become less dependent on the strength of single year-classes. As the dependency on incoming year-classes is reduced at low fishing mortality levels

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such as those generated by the $F_{0.1}$ strategy, our ability to predict future commercial catches should, at least in theory, be improved.

In this paper, we focus on the accuracy of catch projections. The basic scientific data for the assessment of fish stocks include catch and weight information, biomass estimates from research surveys, and information on commercial catch rates. Analytical models are used for integrating the information originating from these various sources. In a study of the performance of assessments carried out on eight groundfish stocks of the Northwest Atlantic, Rivard (1981) observed a maximum difference of more than 33% (on average) among estimates of stock size produced in three consecutive assessments. A relative error of 15% was calculated for Atlantic cod in NAFO Divisions 4T-Vn, and for that stock, more than 60% of the variance was due to the uncertainties associated with the estimates of mean weights-at-age. Subsequently, Rivard (1983) analyzed, using Monte Carlo simulations, the impact of systematic, analytical, and sampling errors in catch-at-age, mean weight-at-age, and the stock size index on the results of an assessment. In the case studied — the simulated stock had the biological characteristics of a cod stock of the Northwest Atlantic — the author concluded that the variance of the projected catch was principally due to errors associated with the mean weights-at-age and with the independent index of stock size used to calibrate the sequential population analysis.

In their simulation of three North Sea fish stocks, Pope and Gray (1983) investigated the relationship between the precision of the input data and the precision of the TACs for three different methods, namely (1) the estimation of status quo TACs, i.e. a TAC established under the assumption that the fishing mortality in the projection year is the same as the fishing mortality achieved in the current year, (2) the determination of TACs from projections at a reference fishing mortality level, F_{MAX}, and (3) the determination of TACs from projections at a fixed arbitrary fishing mortality level. Their estimate of the coefficients of variation for TAC estimates was 12−25% for North Sea plaice, 27−33% for North Sea cod, and 39−53% for North Sea sprat.

In his evaluation of the level of accuracy/precision for various groundfish stocks evaluated by the International Council for the Exploration of the Sea (ICES), Brander (1985) concluded "Whatever the merits of TACs and quotas as a means of allocating shares in a stock to the different countries or fishing interests participating, it must be recognized that the present level of variability in assessments carried out in the previous year makes them an imprecise tool for achieving desired levels of fishing mortality." In view of the uncertainties about recruitment, fishing mortality, and catch composition in the intermediate year, Brander recommended that forecasts be carried out for the current year only. This statement was made in the context of fish stocks which experience much higher fishing mortalities than those encountered by most Canadian groundfish and pelagic stocks in the Northwest Atlantic. Brander (1985) does not provide insight into the impact of such uncertainties when much lower fishing mortality rates are prevalent.

The past performance of catch projections is evaluated below in a retrospective analysis of the assessments for a number of groundfish and pelagic stocks of the Northwest Atlantic. Variances of stock size, mean weight-at-age, catch-at-age, and recruitment estimates used in catch projections are also estimated and their impact on catch projections are evaluated. Our purpose is to identify the parameters of importance for catch projections and to develop recommendations for improving their accuracy.

Methods

For many of the groundfish and pelagic stocks of the Northwest Atlantic, the TAC is based on the results of a projection model which uses the most recent information on growth, partial recruitment, and stock size (population abundance) and on estimates of recruitment for the projection period. In a typical assessment, a 2-yr projection is carried out. In general, the following assumptions are made for the calculation of TACs from input parameters (i.e. stock size, $N_{i,t}$; catch-at-age, $C_{i,t}$; mean weight, $W_{i,t}$; recruitment R_{t+1} and R_{t+2}, where i refers to age and t to year): yield is projected for year $t + 2$, assuming that the TAC for year $t + 1$ will be taken; the mean weights, $W_{i,t}$, used in the projection $t + 1$ and $t + 2$, are those estimated for year t; and the recruitments, R_{t+1} and R_{t+2}, are estimated from a long-term average calculated from virtual population analysis (VPA). The projection algorithm used in a typical assessment is described in detail in Rivard (1982).

Retrospective Analysis

Our analysis of the performance of past projections is based on the study of 18 fish stocks of commercial importance in the Northwest Atlantic. Among groundfish species, our study covers six stocks of Atlantic cod (*Gadus morhua*), two stocks of haddock (*Melanogrammus aeglefinus*), and one stock each for redfish (*Sebastes* sp.), yellowtail flounder (*Limanda ferruginea*), American plaice (*Hippoglossoides platessoides*), and pollock (*Pollachius virens*). Among pelagic species, it covers five stocks of herring (*Clupea harengus*) and one stock of Atlantic mackerel (*Scomber scombrus*).

In order to assess the performance of past projections, we compared the 1980 TACs calculated in 1979 (using 1978 data) and the 1982 TACs calculated in 1981 (using 1980 data) with the catch projected at $F_{0.1}$ using the most recent information on stock size, mean weight, and partial recruitment coefficients (for simplicity, the most recent estimates are referred to as the "true" quantities). In order to maintain some objectivity in this comparison, the following procedure was adopted. A 1-yr (or within year) projection was made, using as input (1) the stock size estimate at the beginning of the assessment year (1979 and 1981), as estimated in the most recent assessment (usually, the 1985 assessment), and (2) the mean weights-at-age for the assessment year, as presented in the most recent information. The partial recruitment coefficients were derived from the matrix of fishing mortality calculated in the most recent assessment. In most cases, to prevent small errors at older ages from systematically lowering all partial recruitment coefficients, fishing mortalities were smoothed by using medians of 3, repeated until convergence (i.e. the A3R method of McNeil 1977); the smoothed fishing mortalities were then standardized to unity to give the partial recruitment coefficients. For the projection, the $F_{0.1}$ value corresponding to the true partial recruitment vector and the true mean weights-at-age was calculated.

Natural mortality was fixed arbitrarily at the same level currently adopted by CAFSAC for the various species. The results of this calculation of the $F_{0.1}$ catch were compared with the 2-yr projections made by CAFSAC. As more than one option is often explored in calculating reference catch levels,

TABLE 1. Source references and methods used in calculating variances of input parameters used in catch projections. Abbreviations: NAFO = Northwest Atlantic Fisheries Organization; CV = coefficient of variation; VPA = virtual population analysis.

Stock		Input parameter			
Species	NAFO area	Catch-at-age	Weight-at-age	Recruitment	Initial stock size
Cod	3Pn-4RS	Calculated using CVs estimated for 1982 catch given in Gavaris and Gavaris (1983) and Gascon (1983)	Calculated from Table 12b in Gascon (1984) for 1977–83.	Calculated from VPA of Gascon (1984) for 1974–83.	CV of 9–13% estimated in VPA tuning regression of Gascon (1984). CV of 11% used in our analysis
Cod	4T-Vn	CVs assumed to be equal to average of CVs estimated for cod stocks	Calculated from table 9 of Lever and Waite (1984) for 1971–83	Calculated from VPA of Lever and Waite (1984) for 1971–83	CVs of 15–18% for ages 6–9; 20–25% for others were estimated in survivor analysis of Lever and Waite (1984)
Cod	4VsW	CVs used were those estimated for the 1984 catch by Sinclair and Gavaris (1985)	Calculated from historical mean weights for 1965–83 given in Gagné et al. (1984)	Calculated from VPA of Gagné et al. (1984) for 1958–83	CV of 11% was used as was suggested by the VPA tuning regression of Gagné et al. (1984)
Haddock	4VW	CVs assumed equal to averages estimated for cod stocks	Calculated from table 15 of Mahon et al. (1984) for 1970–83	Calculated from VPA of Mahon et al. (1984) for 1971–83	CV of 35% used given poor tuning of VPA reported by Mahon et al. (1984)
Haddock	4X	CVs assumed to be equal to averages estimated for stocks	Calculated from table 7 of O'Boyle et al (1984) for 1970–83	Calculated from VPA of O'Boyle et al. (1984) for 1962–82 for age 1	CVs of 50–55% as estimated in survivor analysis of O'Boyle et al. (1984) were used
Pollock	4VWX + SA5	CVs assumed to be equal to averages estimated for cod stocks	Calculated from table 9 of McGlade et al. (1984) for 1974–83 for ages 2–11	Calculated from VPA of McGlade et al. (1984) for 1974–82 for age 2	CV of 20% was estimated from VPA tuning regressions of McGlade et al. (1984)
Redfish	4RST	Calculated using CVs estimated for 1982 catch given in Maguire et al. (1983)	Calculated from table 7 of Rubec et al. (1984) for 1980–83 for ages 5–29	Calculated from VPA of Maguire et al. (1983) for 1972–80 for age 5	CV of 18% estimated from VPA tuning regression of Rubec et al. (1984)
Herring	4T	CV assumed to be 10%	Average of relative error of spring and fall spawners, calculated from tables 7 and 8 of Ahrens (1985) for 1971–76 for ages 2–11+	Average of relative error of spring and fall spawners, calculated from VPA of Ahrens (1985) for 1971–83 for age 2	CV of 26% for fall spawners estimated from VPA tuning regressions of Ahrens (1985)
Herring	4R	CV assumed to be 10% for each age group	Average of relative error of spring and fall spawners, calculated from table 12 of Cleary and McQuinn (1984)	Average of relative error of spring and fall spawners (130%), calculated from VPA of Cleary and McQuinn (1984)	CV of 22% estimated from VPA tuning regression for fall spawners

we have (except where otherwise indicated) used the projection which assumed that the catch in the first year of the projection was equal to (or closest to) the TAC adopted for that year. The reader should note that because the TAC initially set from the 2-yr projection is often revised in a subsequent assessment, the projected catches reported herein may deviate from the final TAC advised.

A measure of the relative contribution of each source of error was obtained in the following manner. A TAC, say TAC_x, was computed with the "true" values for each variable, except for variable x which was assigned the value originally used in the assessment. Then a measure of the impact of variable x on the observed difference in TAC was calculated as

$$\frac{TAC_x - TAC_{true}}{TAC_{true}} \times 100.$$

In order to attain an overall impression of the contribution of each input variable to overall error, a global impression scale was developed for the stocks studied. A contribution index (CI)

TABLE 2. Estimates of the 1980 and 1982 catch at $F_{0.1}$ for some commercial stocks of the Northwest Atlantic, as initially projected and as back-calculated from the results of the 1985 assessments.

		1980			1982		
Species	Stock	Projected	Back-calculated	Relative difference (%)	Projected	Back-calculated	Relative difference (%)
Cod	2J-3KL	212 000	144 350	46.9	270 000	207 410	30.2
	3NO	16 500	22 760	−27.5	20 000	23 857	−16.2
	3Ps	28 000	18 834	48.7	33 000	17 814	85.2
	3Pn-4RS	59 000	58 310	1.2	105 000	75 540	39.0
	4TVn[a]	63 000	20 699	204.4	65 000	32 945	97.3
	4VsW	45 000	31 338	43.6	53 000	23 613	124.5
Haddock	4VW	15 000	8 461	77.3	24 000	7 127	236.7
	4X[b]	28 000	17 436	60.6	32 000	12 655	152.9
Redfish	4RST[c]	18 000	59 094	−69.5	31 000	76 571	−59.5
Yellowtail flounder	3LNO	18 000	8 509	111.5	23 000	5 413	324.9
American plaice	3LNO	43 400	41 419	4.8	45 000	15 581	188.8
Pollock	4VWX-5	41 750	47 403	−11.9	55 000	32 589	68.8
Herring	4WX[d]	83 000	68 514	21.1	92 000	74 344	23.7
	4T, spring[e]	50 102	8 992	457.2	20 000	31 831	−37.2
	4T, fall[e]	39 271	11 332	246.5	—	—	—
	4R, spring[f]	13 160	23 497	−44.0	8 202	11 547	−29.0
	4R, fall[f]	4 911	5 841	−15.9	4 542	4 058	11.9
Mackerel	2-6[g]	197 000	176 710	11.5	118 000	97 700	20.8
Overall		975 094	773 499	26.1	998 744	750 595	33.1

[a]The TAC was revised to 54 000 t for 1980 and to 60 000 t for 1982.
[b]A 1-yr projection was done for 1980.
[c]The projections for 1979 were considered to be indications only because of the unreliability of the data.
[d]The 1980 projection was revised to 65 000 t.
[e]The $F_{0.1}$ projections were not the recommended options for 1980; instead, a strategy to reduce the decline of the stock was recommended.
[f]A 1-yr projection was done for both 1980 and 1982.
[g]The value of 118 000 t for 1982 corresponds to one of many options explored.

was first assigned to each variable from its contribution to overall error:

CI	Contribution to error in % (range)
0	0−15
1	16−30
2	31−60
3	61−90
4	>90

A global contribution index for variable x (GCI_x) was calculated as the summation of the CIs for all stocks.

Calculation of Variances

While the variances of input quantities are not presented in every assessment, it is often possible to estimate them from the assessment data. The study of variances covered three cod stocks, two stocks of haddock, one of pollock, one of redfish, and two of herring. Specific stocks are listed in Table 1, together with data sources and assumptions used in estimating variances. Variances have been estimated in the following manner for catch-at-age, mean weight, recruitment, and stock size.

Variance of catch-at-age

Variances for catch-at-age were calculated using the method of Gavaris and Gavaris (1983), which assumes that the proportion at length is a multinomial variate. It should be noted, however, that recent developments suggest that the above method for calculating the variance of catch-at-age generally gives estimated coefficients of variation which may be somewhat lower than the actual values (S. Gavaris, Department of Fisheries and Oceans, Fisheries Research Branch, St. Andrews Biological Station, St. Andrews, N.B., pers. comm.). The variance of catch-at-age is thus likely to have been underestimated by the method used.

Variance of mean weight-at-age

The variance of mean weight-at-age appears as a result of both stochastic errors and sampling errors. Stochastic error is present because we do not have a reliable equation to describe changes in growth over time. The variance of the mean weights was estimated from the relative error observed in historical data. As the current practice is to use the weights in year t to project catches in year $t + 2$, the average relative error for a given age i has been defined as

$$\bar{e}_i^2 = (1/k)\ \mathrm{SUM}\ [(W_{i,t} - W_{i,t+2})^2/(W_{i,t+2})^2]$$

where the summation is over t (time) and where k is the number of elements in the summation (Rivard 1981). Then, the average relative errors were used to estimate the variance of mean weight for each age-group in the projection, i.e.

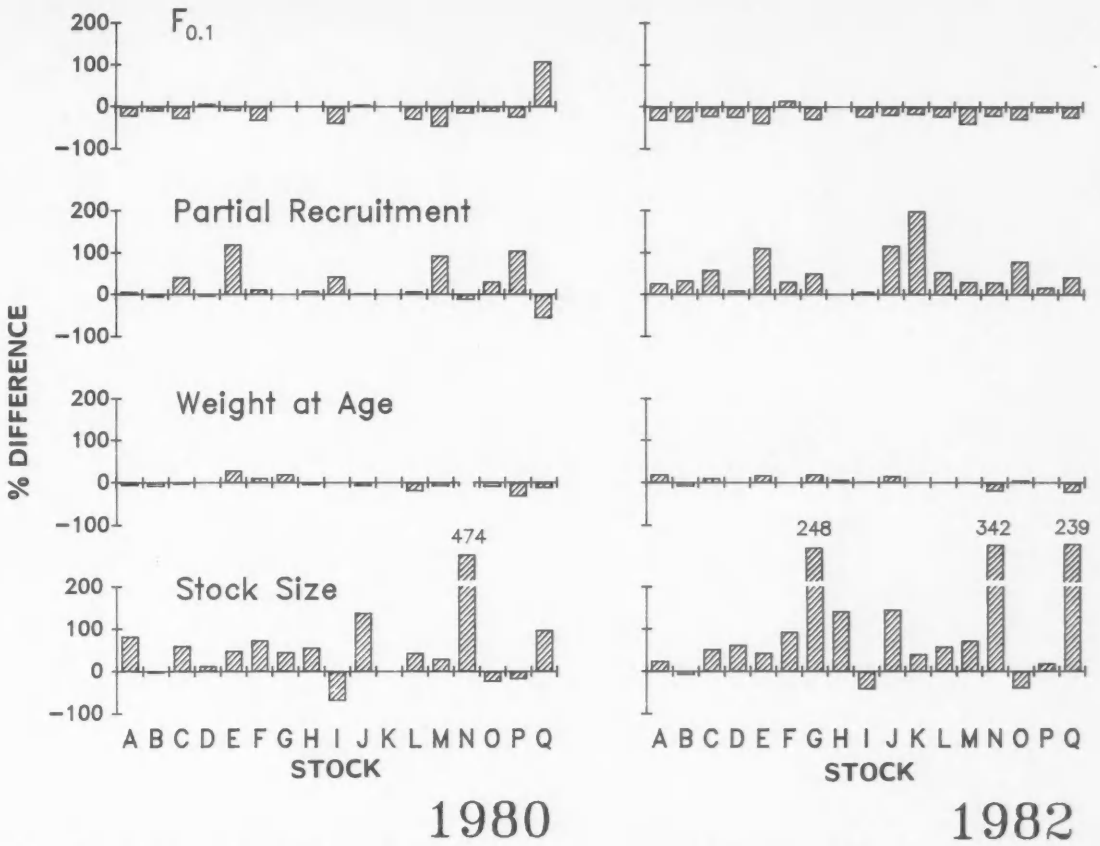

FIG. 1. Anatomy of relative differences between the projections provided in previous assessments and the $F_{0.1}$ catch calculated from the results of the 1985 assessments. The stocks are cod (A−F), haddock (G−H), redfish (I), flatfish (J−K), pollock (L), herring (M−P), and mackerel (Q).

$$\text{VAR}[W_i] = (W_i \times \bar{e}_i)^2$$

for each age i.

Variance of recruitment

The relative error on recruitment prediction was estimated from the ratio of the standard deviation of recruitment to mean recruitment. Estimates of recruitment were obtained from the results of virtual population analyses (Table 1). The number of observations included in the calculation of the relative error in recruitment varied between 9 and 26. As the years covered by these observations are representative only of the recent history of these stocks, the estimates of relative error in recruitment prediction must be seen only as a measure of recruitment variability in recent times.

Variance of stock size-at-age

Estimates of stock size for the first year of the projection period are the result of a complex procedure (see Rivard 1983). As regression analyses are used for the *calibration* of virtual population analysis, we have assumed, for estimating variances of initial stock size, that the confidence intervals of the stock size predicted by the regressions provide an appreciation of the precision of the stock size estimates. This assumes that the independent variable of the calibration regression is known without error, or has a measurement error which is much smaller than the measurement error in the dependent variable. Such an assumption is implicit in most assessments. In addition, a measure of the precision (variance) of stock size estimates has been obtained from the SURVIVOR method (Doubleday 1981) for certain stocks. Finally, when more than one method is used for estimating the initial stock size, the range of values obtained from these different methods has been used to calculate the relative error.

Variance of catch projections

We have used the approach of Rivard (1981) for calculating the variance of catch projections from the variance of input parameters. The variance of the yield projected for year $t + 2$, say Y_{t+2}, has been calculated as:

$$\begin{aligned}\text{VAR}[Y_{t+2}] = {} & \text{SUM VAR}[N_{i,t}](\partial Y_{t+2}/\partial N_{i,t})^2 \\ & + \text{SUM VAR}[C_{i,t}](\partial Y_{t+2}/\partial C_{i,t})^2 \\ & + \text{VAR}[R_{t+1}](\partial Y_{t+2}/\partial R_{t+1})^2 \\ & + \text{VAR}[R_{t+2}](\partial Y_{t+2}/\partial R_{t+2})^2 \\ & + \text{SUM VAR}[W_{i,t}](\partial Y_{t+2}/\partial W_{i,t})^2\end{aligned}$$

where all summations are over i. This equation assumes that there is no significant covariance between input parameters and that the partial recruitment coefficients are known exactly for the projection years $t + 1$ and $t + 2$.

In this study, the *prerecruited* age-groups were defined as those age-groups for which the partial recruitment coefficient was less than 0.3. This value was chosen because stock size is difficult to estimate for age-groups showing a partial recruitment coefficient smaller than 0.3. Such a definition is necessary to allow comparisons of variances between species or species groups.

Results

Retrospective Analysis

The results of the retrospective analysis (Table 2) indicate considerable differences between projected catch levels and the actual $F_{0.1}$ catches for the two years studied. The deviations from the $F_{0.1}$ catch are often large and there is a general tendency to be optimistic, i.e. to overestimate the $F_{0.1}$ catch. The overall error level for all stocks tested is +26.1% for 1980 and +33.1% for 1982. Most frequently, advised TACs resulted in a much higher fishing mortality rate than $F_{0.1}$. It is somewhat surprising to see that the relative difference between the projected and the true TACs is small for a stock like 3NO cod for which the quality of assessment data is currently questioned. The fact that the retrospective analysis did not identify major differences between the projected and the *true* TACs for some stocks does not necessarily imply that a high accuracy is achieved for these stocks. The differences may be small in certain cases because the basic data are limited and thus less likely to lead to divergent interpretations.

The major sources of error which contributed to the differences between the advised TAC and the true catch at $F_{0.1}$ were examined. The errors can be attributed to differences in partial recruitment coefficients, mean weight-at-age, stock size estimates for year 2 of the projections, and the $F_{0.1}$ value utilized (Fig. 1). The origin or causes of error in the projections which we examined were, in order of importance, as follows. (1) The estimation of stock size for the last year of the projection period. This can be influenced by several sources of error: (i) the estimation of population abundance from the virtual population analysis; (ii) difference between the TAC in the first year of the 2-yr projection and the actual catch in that year; (iii) difference between the catch composition in the first year of projection and the actual catch composition in that year; and (iv) differences in estimations of recruiting cohorts during the projection period. (2) The changes or variations in partial recruitment coefficients. These may be due to (i) estimation errors or (ii) external changes in fleet behavior, gear types, seasonality of the fishery, etc. (3) The estimation of $F_{0.1}$ for the projection years.

Errors in estimation of mean weights-at-age appeared to contribute little to overall error in the catch projections. The errors in the coefficients of partial recruitment and in $F_{0.1}$ were often compensatory or of opposite sign. This results from the fact that $F_{0.1}$ is itself estimated from the estimates of partial recruitment and that $F_{0.1}$ appears as a multiplier to the partial recruitment in the projection algorithm. Thus, in a particular assessment, it is the combined effect of $F_{0.1}$ and partial recruitment that is important.

The overall contribution of each variable to error in catch projections, as measured by the GCI, is illustrated for each species in Fig. 2 and for the two common groupings, groundfish and pelagic fish, in Fig. 3. Note that errors attributable to the estimation of $F_{0.1}$ and partial recruitment have been combined to illustrate the overall error in reference fishing mortality (i.e. $F_{0.1}$ × partial recruitment).

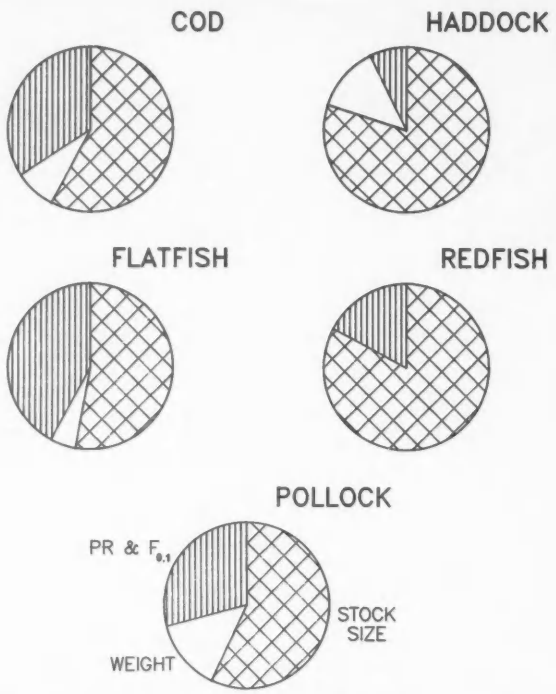

FIG. 2. Relative contribution of each input variable to error in catch projections for cod, haddock, flatfish, redfish, and pollock, based on the global contribution indices (GCIs).

Sources of error tend to vary considerably between stocks (Fig. 1) and between species (Fig. 2). Inaccuracies in the catch projections of cod are largely attributable to errors in estimation of stock size and reference fishing mortalities (partial recruitment × $F_{0.1}$) for the projection period. Similarly, pollock and flatfish projection inaccuracies can be related to changes in stock size and reference fishing mortalities. Errors in haddock and redfish projections result largely from changes in stock size. Errors in estimating age-specific mean weights appear to contribute relatively little to the total error.

Variance of Input Parameters

The overall precision of projected catches is affected by both *sampling errors* and *stochastic errors*. Because the quantities serving as input to catch projections cannot be enumerated exhaustively, we must rely on a sampling scheme to estimate them. Consequently, sampling errors are a function of the intensity of catch sampling programs and of the coverage of research surveys. In general, when sampling is carried out according to a predetermined design (such as a random stratified design), sampling errors can be evaluated from sampling theory. The other type of error, stochastic error, is the result of "natural" variability and is independent of sampling programs.

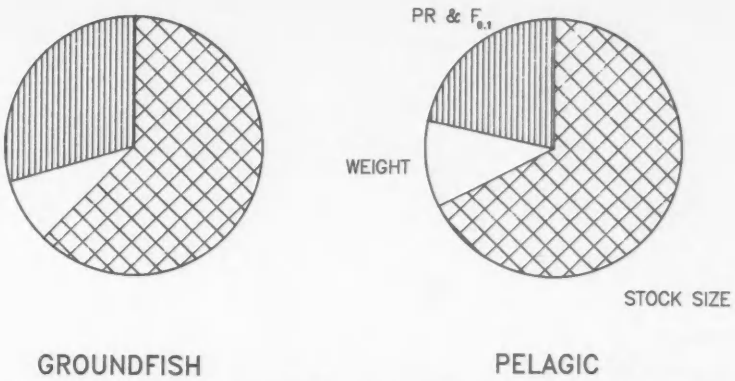

FIG. 3. Relative contribution of each input variable to error in catch projections for groundfish and pelagic fish of the Northwest Atlantic, based on the global contribution indices (GCIs).

TABLE 3. Coefficient of variation (%) for catch-at-age estimates for 10 Atlantic Canada fish stocks. Data sources: Gavaris and Gavaris (1983); Gavaris and Bishop (1983); Bishop and Gavaris (1983); Gascon (1983); Brodie and Pitt (1983a, 1983b, 1983c); Maguire et al. (1983); Atkinson (1983a, 1983b); Sinclair and Gavaris (1985).

	Cod					American plaice			Redfish		
Age	4RS-3Pn (1981)	4RS-3Pn (1982)	2GH (1982)	3Ps (1982)	4VsW (1984)	3LNO (1982)	2J-3K (1982)	3Ps (1982)	4RST (1982)	3P (1982)	2 + 3K (1982)
2	52	—	—	61	81	—	—	—	—	—	—
3	20	20	7	27	13	—	—	—	—	—	—
4	4	10	8	4	4	—	—	—	—	—	—
5	5	4	10	6	3	33	—	—	—	—	—
6	3	6	11	8	4	22	71	66	—	—	—
7	4	5	4	5	4	12	32	23	17	46	21
8	6	6	6	4	6	7	19	18	15	21	12
9	8	9	3	9	9	4	13	12	11	12	10
10	12	11	14	12	12	4	10	7	14	16	10
11	15	13	33	23	10	4	9	5	10	14	10
12	15	19	47	19	12	4	11	9	12	12	10
13	16	26	27	29	16	5	11	11	13	11	10
14	22	28	38	33	19	6	14	11	14	10	11
15	31	40	43	39	49	7	19	18	15	11	10
16	—	—	—	—	19	9	29	19	18	12	10
17	—	—	—	—	—	15	55	22	22	15	10
18	—	—	—	—	—	18	63	21	30	18	11
19	—	—	—	—	—	72	—	—	32	18	12
20	—	—	—	—	—	—	—	—	28	25	14
21	—	—	—	—	—	—	—	—	27	20	13
22	—	—	—	—	—	—	—	—	22	19	18
23	—	—	—	—	—	—	—	—	18	21	17
24	—	—	—	—	—	—	—	—	12	16	16
25	—	—	—	—	—	—	—	—	18	15	19
26	—	—	—	—	—	—	—	—	14	13	18
27	—	—	—	—	—	—	—	—	19	16	19
28	—	—	—	—	—	—	—	—	20	16	21
29	—	—	—	—	—	—	—	—	27	18	21
30	—	—	—	—	—	—	—	—	—	10	9

The coefficients of variation for catch-at-age estimates have been produced for a number of stocks in Atlantic Canada (Table 3). Typically, the coefficients of variation for the dominant ages in the catch are in the order of 3−6% for cod stocks, 4−10% for American plaice stocks, and 10−15% for redfish stocks. The coefficients of variation are larger for very young ages and for older age-groups.

The error made in mean weight-at-age is related to the fact that the weights calculated for year t are used to forecast the mean weights for years $t + 1$ and $t + 2$. This error has two components: a sampling component, due to the fact that the weights in year t are estimated from sampling data, and a stochastic component, due to *external* factors affecting mean weight in a given year (fishery being prosecuted in different

TABLE 4. Relative error (%) in weight-at-age estimates for 10 stocks of the Northwest Atlantic. Data sources: see Table 1, and Simon and Campana (1984) for 4Vn herring.

	Cod			Haddock		Pollock	Redfish	Herring				
Age	4RS-3Pn	4T-Vn	4VsW	4VW	4X	4VWX	4RST	4T, spring	4T, fall	4Vn	4R, spring	4R, fall
2	—	—	35	47	20	33	—	13	19	—	—	—
3	—	33	20	19	13	33	—	16	31	13	18	21
4	25	14	14	12	11	30	—	2	10	16	11	18
5	16	16	13	11	13	12	15	3	11	7	10	13
6	8	19	14	12	13	11	15	5	24	8	11	10
7	4	28	15	12	14	10	15	6	9	8	13	14
8	7	36	18	17	14	13	12	4	12	7	12	12
9	13	37	16	8	13	10	12	7	11	7	11	11
10	19	45	16	13	11	11	11	5	10	7	11	16
11	25	42	18	18	12	11	8	8	9	—	11	12
12	49	29	19	—	19	—	5	—	—	—	—	—
13	22	31	20	—	16	—	3	—	—	—	—	—
14	34	42	18	—	—	—	3	—	—	—	—	—
15	35	114	19	—	—	—	5	—	—	—	—	—
16	—	—	19	—	—	—	1	—	—	—	—	—
17	—	—	—	—	—	—	7	—	—	—	—	—
18	—	—	—	—	—	—	4	—	—	—	—	—
19	—	—	—	—	—	—	18	—	—	—	—	—
20	—	—	—	—	—	—	21	—	—	—	—	—
21	—	—	—	—	—	—	20	—	—	—	—	—
22	—	—	—	—	—	—	24	—	—	—	—	—
23	—	—	—	—	—	—	21	—	—	—	—	—
24	—	—	—	—	—	—	18	—	—	—	—	—
25	—	—	—	—	—	—	15	—	—	—	—	—
26	—	—	—	—	—	—	16	—	—	—	—	—
27	—	—	—	—	—	—	8	—	—	—	—	—
28	—	—	—	—	—	—	10	—	—	—	—	—
29	—	—	—	—	—	—	5	—	—	—	—	—
30	—	—	—	—	—	—	—	—	—	—	—	—

time of year, differences in growth, effects of density dependence, etc.). The error made in mean weight can be important (Table 4). For dominant age-groups in the catch, it varies from 4 to 20% for the cod stocks examined, from 10 to 15% for the haddock stocks, from 1 to 7% for redfish, and from 2 to 14% for herring.

The ratio *standard deviation/mean recruitment* was in the order of 0.3–0.7 for cod stocks, 1.0 for haddock, 0.5 for redfish, 0.7 for pollock, and 0.6–1.3 for herring. In other words, herring and haddock stocks showed the largest recruitment variability. These results are not surprising, since the fisheries on these stocks often depend on a single or a few strong year-classes.

Uncertainties in stock size estimates originate from the application of VPA, which combines information from research surveys, commercial catch sampling, and logbooks. The coefficients of variation for stock size estimates are presented for some stocks of the Northwest Atlantic in Table 1.

Variance of Catch Projections

The variance of catch projections, expressed in terms of coefficient of variation, for the major commercial fish stocks of the Northwest Atlantic is illustrated in Fig. 4. The coefficients of variation of the catch projected at $F_{0.1}$ were as follows: 15–20% for cod stocks; 25–50% for haddock; 28% for pollock; 16% for redfish; and 35–42% for herring. These coefficients provide an indication of the precision of the projected catches (assuming no biases are present) when the assessment procedure described above is applied. These coefficients are likely to be underestimated, since the variance of catch-at-age is likely to have been underestimated (see below).

The contribution of each of the input parameters to the total variance of catch projections is also illustrated in Fig. 4. For two of the cod stocks studied, the variance in initial stock size was the main contributor to total variance of projected catches. For the third cod stock, the variance in mean weight-at-age and the variance in prerecruit estimates were the main components of total variance. The precision of catch projections for the two haddock stocks showed a strong dependence on the variance in prerecruit estimates. This is consistent with the observation that these haddock stocks were fished at fishing mortality rates approaching F_{MAX} during a period of rapid recovery at the end of the 1970s. For one of the haddock stocks, the variance in stock size also made a large contribution to the variance of the projections. For pollock and redfish, the major component of variance was that of stock size estimates; recruitment estimates and stock size estimates for prerecruited age-groups had little impact on the precision of catch projections. Similarly, the variance of mean weight-at-age contributed little to the overall variance of catch projections for these two species. The variance of catch projections for herring had two major components: the variance of stock size estimates and the variance of recruitment and prerecruit estimates. From these observations, it appears that for any given stock only a few input parameters

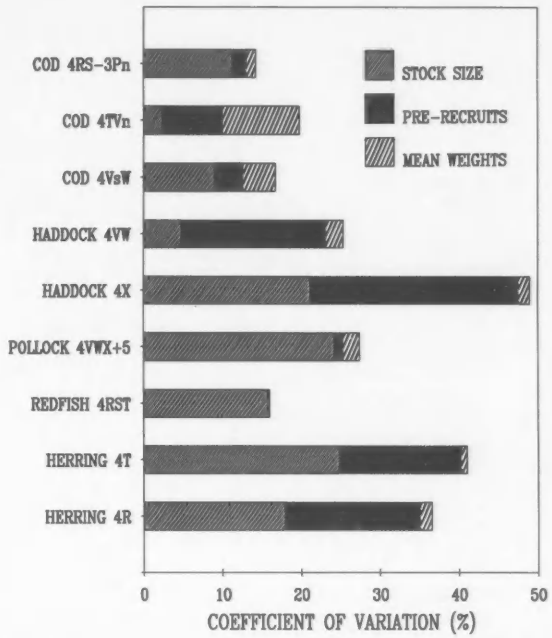

FIG. 4. Components of variance for catch projections of various Atlantic Canada fish stocks. The variance components are expressed in terms of their contribution to the coefficient of variation. The coefficient of variation for catch-at-age was less than 1% for all stocks and is not illustrated. See Table 1 for data sources.

contribute significantly to the variance of catch projections and that these vary among stocks. Consequently, there is no unique approach/solution for improving the overall precision of catch projections.

In general, catch-at-age contributed little to total variance. It must be noted, however, that uncertainties in catch-at-age appear explicitly in the projection model only for the first year of the projection period and that part of the variance calculated for stock size estimates is due to uncertainties in catch-at-age, as catch-at-age enters the calculation of stock size through VPA. In effect, the *variance of stock size* is the result of sampling errors from research surveys, logbook information, and commercial catch sampling programs.

Sources of Bias in Catch Projections

The variance of projected catches was calculated under the assumption that the driving variables were known exactly for the projection period. The driving variables are (1) the catch level for the first year of projection, (2) the age composition for the first year of the projection period (implied from the partial recruitment coefficients), and (3) the fishing mortalities (partial recruitment coefficients $\times$ $F_{0.1}$) for the second year of the projection period. These variables are rarely known exactly. In general, the errors they contain are not random but systematic. Consequently, these errors translate as biases into catch projections.

Catch in the first year of projection

In general, a 2-yr projection assumes that the catch level for the first year is equal to the TAC advised for that year. Often, the real catch level is quite different from the TAC advised, as indicated in Table 5. There are two reasons for these differences: firstly, the advised TAC in the first year may have been updated in a subsequent projection, and secondly, the actual catch from the stock may have been higher or lower than the advised TAC. We investigated the effect of such factors upon the projections carried out in 1979 and 1981 for the 1980 and 1982 fishing seasons, respectively. For those years, the catch projections were made under the assumption that the catch level for the first year of the projection period was equal to the nominal catch reported. Results (Table 6) indicate that the error made in the catch level for the first year of the projections is not a major source of error for a 2-yr projection. The only stock in which a major error was introduced because of this factor was mackerel in SA 2–6. For this stock, the projection assumed catch levels of 259 000 and 151 000 t for 1979 and 1981, respectively, while the actual catch in those years was approximately 30 000 t.

Catch composition for the first year of the projection period

In a 2-yr projection, the catch composition for the first year of the projection period is implied from the values of the partial recruitment coefficients (see Rivard 1982). The assumed and the actual catch compositions for year 1 of the projection are known to be different in many cases. Figure 5 illustrates two particular cases.

For stocks that showed a large difference between the assumed and the actual partial recruitment pattern, we evaluated the impact of changes in age composition on the TAC calculations (Table 7). Errors in catch composition for the first year of the projection period did not have, in general, a significant impact on catch projections. The impact on reference catch estimates is small because, under current fishing strategies, the catch represents a small fraction of the total stock biomass, and consequently, any variation in the age composition of the catch changes only slightly the age composition of the stock itself.

Fishing mortalities for the second year of the projection period

From the retrospective analysis (Fig. 1), partial recruitment coefficients appear to be a major source of bias in 2-yr projections. Problems in the estimation of partial recruitment can be further described as follows. The current practice, in making catch projections, is to use the partial recruitment estimated for the latest year or an average based on recent data. As partial recruitment is based on historical data, a lag is introduced between the occurrence of an event in the fishery (such as the arrival of a strong year-class) and its representation in the estimates of partial recruitment. Partial recruitment estimates are not forecasts; they are back-calculations from recent data.

These problems are illustrated in Fig. 6, which uses data for cod in NAFO Divisions 4VsW. For the projection of the 1979 catch level, an almost asymptotic partial recruitment pattern was used but a marked dome appears in the back-calculated partial recruitment. For the projection of the 1980 catch level, the same pattern emerges with the exception that the dome formed by the back-calculated coefficients moves to the right by one age-group. For the projection of the 1981 catch level, a dome-shaped partial recruitment pattern was used, but as this pattern was estimated from historical data in which the peak occurred at younger ages, it does not match the pattern described by the back-calculated values. For the projection of the 1982 catch level, the partial recruitment pattern used was dome shaped; however, the back-calculated values form a flat-top curve, suggesting a change in the strategy followed by the fleet.

TABLE 5. Nominal catch (t) vs. the catch level (t) assumed for the first year of projection in assessments done in 1979 and 1981 for several stocks.

		1979		1981	
Species	Stock	Used in projection	Nominal catch	Used in projection	Nominal catch
Cod	2J-3KL	170 000	167 000	200 000	171 000
	3NO	25 000	28 000	15 000	24 000
	3Ps	25 000	33 000	30 000	39 000
	3Pn-4RS	75 000	83 000	75 000	98 000
	4TVn	36 000	56 000	53 000	65 000
	4VsW	30 000	40 000	50 000	54 000
Haddock	4VW	3 000	3 000	23 000	20 000
	4X[a]	25 000	25 000	28 000	31 000
Redfish	4RST	16 000	15 000	20 000	21 000
Yellowtail flounder	3LNO	18 000	18 000	21 000	15 000
American plaice	3LNO	47 000	49 000	48 000	50 000
Pollock	4VWX-5	40 000	47 000	54 000	59 000
Herring	4WX	99 000	96 200	112 000	87 700
	4T, spring	52 000	18 000	16 000	22 000
	4T, fall	52 000	30 000	—	—
Mackerel	2-6	259 000	31 000	168 000	32 000
All groundfish		510 000	564 000	617 000	647 000
All pelagic species		462 000	175 200	296 000	141 700
Overall		972 000	739 200	913 000	788 700

[a]For 4X haddock, a 1-yr projection was done in 1979; the 1979 catch was known at the time of the assessment.

TABLE 6. Estimates of the 1980 and 1982 catch (t) at $F_{0.1}$ as initially projected and as back-calculated under the assumption that the catch in the first year of projection was known.

		1980			1982		
Species	Stock	Initial projection with TAC in 1979	Back-calculated with nominal catch in 1979	Relative error (%)	Initial projection with TAC in 1981	Back-calculated with nominal catch in 1981	Relative error (%)
Cod	2J-3KL	210 000	211 000	−0.5	267 000	272 000	−1.8
	3NO	16 500	16 000	3.1	20 000	18 000	11.1
	3Ps	28 000	27 000	3.7	33 000	31 000	6.5
	3Pn-4RS	59 000	57 000	3.5	105 000	101 000	4.0
	4TVn	63 000	59 000	6.8	65 000	62 000	4.8
	4VsW	45 000	43 000	4.7	53 000	52 000	1.9
Haddock	4VW	15 000	15 000	0.0	24 000	24 700	−2.8
	4X	—	—	—	32 000	31 000	3.2
Redfish	4RST	—	—	—	31 000	30 000	3.3
Yellowtail flounder	3LNO	20 000	20 000	0.0	23 000	25 000	−8.0
American plaice	3LNO	—	—	—	48 000	48 000	0.0
Pollock	4VWX-5	42 000	40 000	5.0	55 000	53 000	3.8
Herring	4WX	82 000	83 000	−1.2	92 000	98 000	−6.1
	4T, spring	50 000	58 000	−13.8	20 000	22 000	−9.1
	4T, fall	39 000	44 000	−11.4	—	—	—
Mackerel	2-6	197 000	277 000	−28.9	118 000	158 000	−25.3
All groundfish		498 500	488 000	2.2	756 000	747 700	1.1
All pelagic species		368 000	462 000	−20.3	230 000	278 000	−17.3
Overall		866 500	950 000	−8.8	986 000	1 025 700	−3.9

Discussion and Conclusions

Three objectives were pursued in this review of catch projections: the documentation of historical performance; the identification of sources of error; and the development of recommendations for future actions.

Error levels in 2-yr projections are significant: the $F_{0.1}$ reference catch levels were overestimated systematically in the two assessment years studied. There is also a certain tendency for reference catch levels to change abruptly. Sudden changes oc-

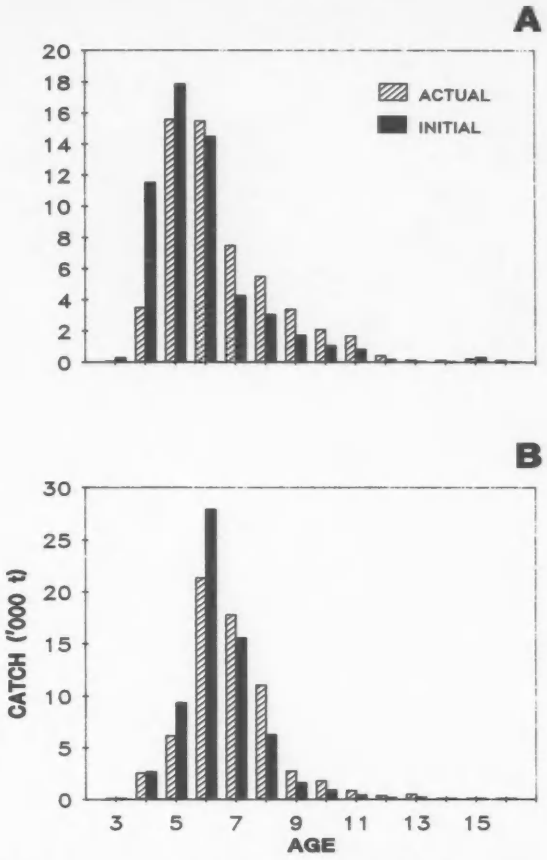

FIG. 5. Comparison of the assumed catch composition for year 1 of the projection period with the actual catch composition for that year. Data are for 4TVn cod in (A) 1979 and (B) 1981.

cur because the variability inherent in assessment data reduces our ability to detect small changes in stock levels. However, accumulated scientific evidence or new information eventually leads to a new interpretation of data, to a revision of stock status, and to a revision of potential catch levels. Sudden changes are more likely to occur when the error content of input variables increases.

The review of historical performance concentrated on "annual errors" and no attempt has been made to measure the accuracy achieved in the long term with 2-yr projections. It is clear, however, that fishing mortality rates have been maintained, in general, below or around F_{MAX} for these Northwest Atlantic stocks, an improvement over the fishing mortalities exerted in the early 1970s. While a relative error of 50 or 60% appears to be a large error for any given year, it may be relatively small if viewed in relation to the catch history of a given stock. For instance, the error of 30–47% for 2J-3KL cod in 1980 and 1982 corresponds to a difference of about 70 000 t between the $F_{0.1}$ catch and the initial projection. This difference is small with respect to catches that could result from the application of excessive fishing mortalities. It is also small with respect to the catches of 500 000 to 700 000 t which took place in the 1960s when the international fleet was competing for fish. In other words, a projected catch level of 270 000 t, despite its inherent error content, still exerts a significant control on fishing effort for this stock.

From our historical review and from our analysis of precision and bias, the following factors emerged as key issues for the projections: dependent on abundance estimates for prerecruited age groups; dependence on stock size estimates for partially recruited and fully recruited age-groups; and dependence on partial recruitment and $F_{0.1}$ estimates for the projection period.

The following did not appear to be major factors for most stocks: the difference between actual catch and assumed catch for the first year of a two year projection; differences in the age composition of the actual and assumed catch for the first year of the projection period; and mean weight-at-age estimates for the projection period.

The impact of each of these sources of error is illustrated in Fig. 7 for all groundfish combined and for herring. While these proportions vary among species (e.g. for haddock, there is higher dependence on the estimation of prerecruited age-groups and recruitment), this illustration conveys a general impression of the relative contribution of each source of error to catch projections.

The retrospective analysis of catch projections is based on the assumption that the VPA has converged to the true stock size. While this assumption is likely to be valid for the cod and haddock stocks studied, it does not necessarily hold for other species (Rivard 1979). For these species, the results of the comparisons made must be interpreted as an indication of the consistency of the projections made in subsequent years.

We have evaluated separately the component of variance due to the abundance estimates of fully recruited age-groups and the component of variance due to the estimation of prerecruited age-groups. It is important to separate these components, as their variance originates from completely different sources. The estimation of abundance for fully recruited age-groups is made through the calibration of VPA. The estimation of prerecruits is made using a wide variety of techniques and is not necessarily linked to VPA. The high dependence of projections for haddock stocks on the abundance estimates of prerecruited age-groups suggests that improving the stock size estimate from the VPA is unlikely to improve the precision of catch projections for this species. It must be noted, however, that the high dependence on prerecruits may be only a transient state for certain stocks. For example, a move towards lower fishing mortalities could reduce the dependence on estimates of prerecruits.

The results of assessments were evaluated here solely on their ability to produce an estimate of the reference catch level. It must be recognized, however, that the value of scientific advice for fisheries management is not limited to the provision of a TAC. In general, scientific assessments also provide information on the performance of the fishery and past history of a stock. In addition, advice generated from the assessment with respect to possible management measures such as gear restrictions, direct effort limitations, or time restrictions (e.g. seasons) is less dependent on the type of quantitative information required for the establishment of a TAC regulation.

Recommendations

The objective of recommendations to improve catch projections should be to reduce errors which contribute significantly

TABLE 7. Relative errors in catch projections due to errors in the catch composition for the first year of the projection period.

		1980			1982		
		Reference catch (t)			Reference catch (t)		
Species	Stock	Back-calculated	With initial catch composition	Relative error (%)	Back-calculated	With initial catch composition	Relative error (%)
Cod	2J-3KL	144 350	145 110	−0.5	207 410	208 288	−0.4
	3NO	22 760	23 026	−1.2	23 857	23 943	−0.4
	3Ps	18 830	19 240	−2.1	17 810	18 160	−1.9
	3Pn-4RS	75 540	75 468	0.1	58 310	58 527	−0.4
	4TVn	20 700	21 608	−4.2	32 940	33 818	−2.6
	4VsW	31 340	31 730	−1.2	23 610	24 125	−2.1
Pollock	4VWX-5	47 400	47 270	0.3	32 590	32 644	−0.2

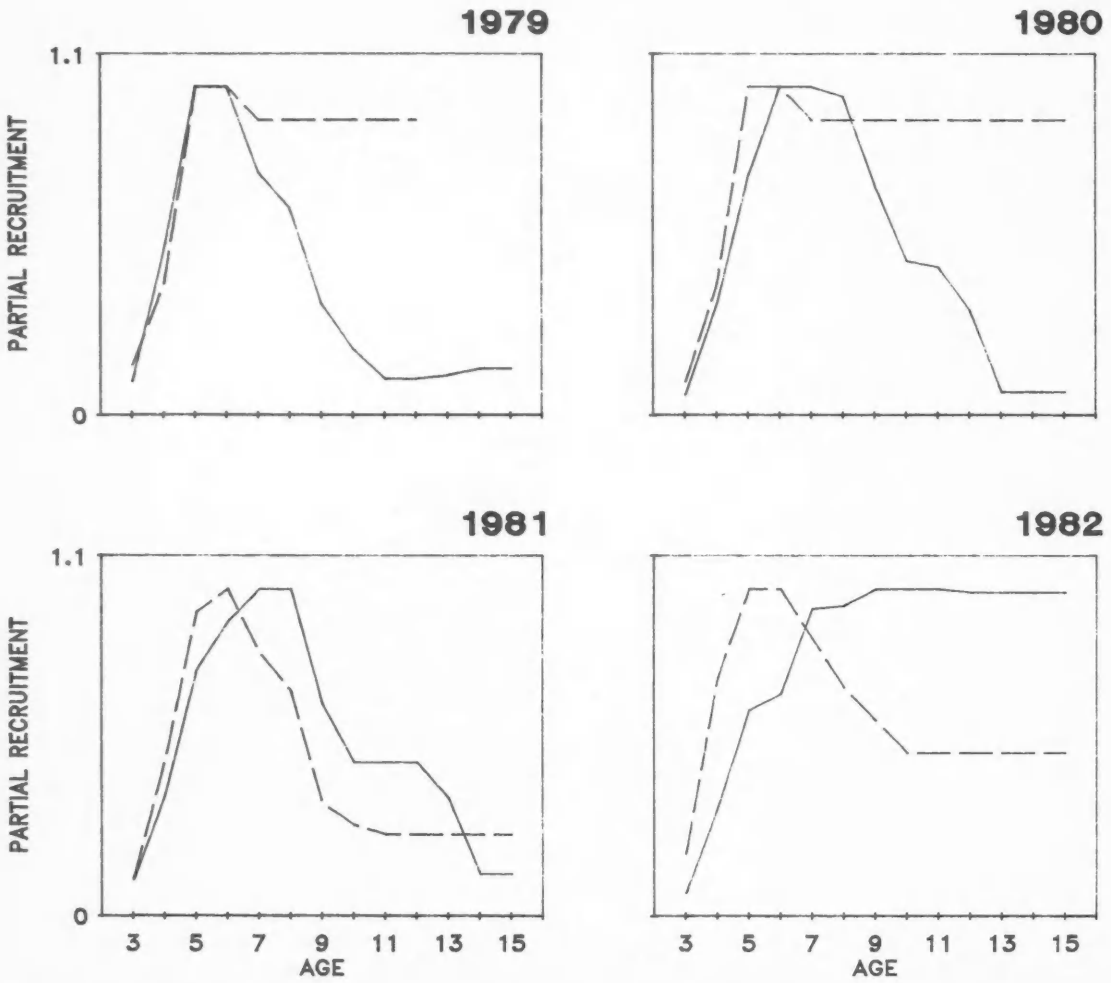

FIG. 6. Comparison of the partial recruitment values initially used (broken line) for catch projections with the values calculated (solid line) from the most recent information. Data are for 4VsW cod.

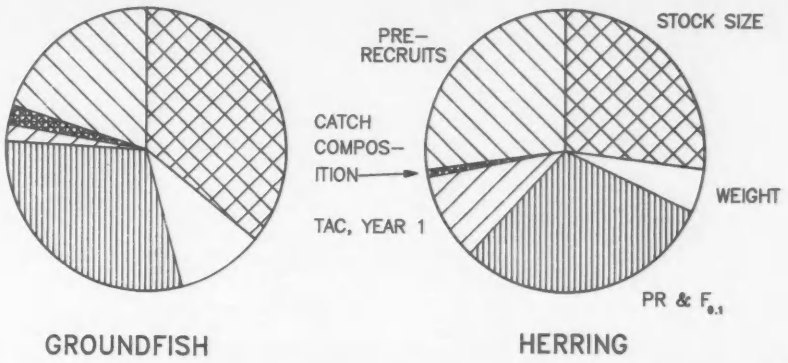

FIG. 7. This composite graph combines the results of the retrospective analysis and those of the study of uncertainties (bias and variance) to illustrate the relative contribution of input parameters to errors in catch projections for groundfish and herring. Note that the category "prerecruits" refers to the abundance of those age-groups for which the partial recruitment coefficients were smaller than 0.3, while the category "stock size" refers to the abundance of the remaining age-groups, i.e. those for which the coefficients were equal to, or higher than, 0.3.

TABLE 8. Recommendations for improving catch projections.

Factor	Recommendation	Program activity or function affected
Estimates of stock size	Improve estimation of stock size obtained from virtual population analysis. Here, there is a wide variety of actions possible:	
	(A) Improve independent measure of stock size (catch rate indices, research survey estimates); related questions are how to combine independent measures when more than one is available and how to resolve conflicting trends in time series	Research surveys; logbook analysis; observer program
	(B) Improve catch composition estimates	Sampling
	(C) Improve methodology: calibration process; need way to cope with variability in survey data; more objective approach	Analysis
Estimates of prerecruited age-groups and of recruitment	Improve estimation of prerecruited age-groups and forecasts of recruitment:	
	(A) Obtain independent measure of abundance	Research surveys
	(B) Better forecasts of recruitment from independent index	Analysis
	(C) Reduce dependence of projections on recruitment by reducing forecast horizon	Scheduling of advice
	(D) Develop stock recruitment relationships	Analysis
	(E) Measure partial recruitment independently of virtual population analysis	Analysis; surveys
Forecasts of fishing mortalities for the projection period	Improve forecasts of partial recruitment coefficients for year 2 of the projection:	
	(A) Develop a model taking into consideration fleet behavior	Analysis
	(B) Do 1-yr projections	Scheduling of advice
	(C) Do multiyear projections which accommodate known levels of error	Analysis
	(D) Other methods/approaches	Analysis

to the accuracy/precision of projections. These sources of error originate from the accuracy/variance of estimates of input variables, such as stock size, partial recruitment, and size of recruiting cohorts, the stochastic nature of some input variables, such as natural mortality and mean weight-at-age, and external changes affecting input variables, such as changes in fishing patterns, in the gear type used, or in the time of year in which the fishery is prosecuted. Because there is no single source of error, there is no simple solution for improving catch projections. Specific ways for improving precision appear in Table 8.

The first source of error, i.e. the estimation of stock size, partial recruitment coefficients, and size of recruiting cohorts, depends on sampling and scientific surveys. Currently, most sampling programs on commercial catches and research surveys are based on norms which were established when Canadian fisheries jurisdiction was extended in 1977. While the norms of NAFO are widely accepted as minimum requirements (Beckett, 1983), sampling based on these norms is not necessarily related to appropriate statistical measures of precision and bias (see Doubleday and Rivard 1981, 1983). Sampling levels should be dictated by target precision levels.

Changes in fleet behavior and fishing pattern result in major changes in partial recruitment coefficients in some years. For instance, a common strategy for a fleet is to adjust their fishing pattern so as to target large cohorts as soon as they become available to the gear and to follow these cohorts in subsequent years; when these cohorts do not provide satisfactory returns, sudden shifts to other age-groups may occur. Similarly, a fleet might avoid an area of good recruitment for a short time and temporarily reduce partial recruitment on specific ages for that year. Changes in partial recruitment for a few age-groups may make a large difference to TAC calculations. While these external factors are generally not under the control of fishery managers, it might be possible, in some instances, to define a model governing the changes in partial recruitment. We presently have sufficient information on certain fisheries to permit a study of fleet behavior in response to changes in recruitment. Such study could serve to define better estimates for partial recruitment during the projection period.

The current approach for catch projections is to project 2 yr ahead. One-year projections (in fact, within-year projections) would reduce the components of error due to recruitment, the abundance of prerecruited age-groups, and to partial recruitment coefficients. One-year projections would be possible, however, only if the assessment could take place before the fishing season. Availability of data on the fishery performance and the lead time required for the establishment of fishing plans may limit the applicability of 1-yr projections for certain stocks. Alternatively, advice can be provided for more than 1 yr. For example, advice could be given for a period of 3–5 yr. From the current knowledge of uncertainties in input data (e.g. catch estimates, mean weights-at-age) and of the natural variability (stochasticity) of some input parameters, it is possible to advise a TAC which would provide a high probability of achieving $F_{0.1}$ despite measurement errors. Reference catch levels (or TACs) would then account for uncertainties and stochasticity in fisheries and biological data. The less that is known about a stock, the more conservative TACs would have to be. Because of this, such an approach may be difficult to implement in an industry which tends to focus on immediate opportunities.

Finally, it must be recognized that a significant proportion of the error in catch projections cannot be reduced by improvements in the model structure, in sampling programs, or in research surveys. For instance, there will always remain a certain amount of error due to the stochasticity of some input variables (e.g. natural mortality, fish availability) or due to unforeseen changes in control variables (e.g. fishing effort and selectivity).

Acknowledgements

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Determination of Population Discreteness in Two Species of Shrimp, *Pandalus jordani* and *Pandalopsis dispar*, from Coastal British Columbia Using Parasite Tags and Other Population Characteristics

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Thompson, A. B., and L. Margolis. 1987. Determination of population discreteness in two species of shrimp, *Pandalus jordani* and *Pandalopsis dispar*, from coastal British Columbia using parasite tags and other population characteristics. Can. J. Fish. Aquat. Sci. 44: 982–989.

Two digenean metacercariae, *Neolebouria tinkerbellae* and an unidentified species (Metacercaria A), parasitizing *Pandalus jordani*, and Metacercaria A parasitizing *Pandalopsis dispar*, were used as naturally occurring biological markers to determine intraspecific population discreteness. Shrimp were sampled from Imperial Eagle Channel and Trevor Channel, Barkley Sound (west coast of Vancouver Island, British Columbia), and from an adjacent offshore area. The mean size at age and the age composition of *P. jordani* and *P. dispar* were also estimated. Many differences occurred among samples in the abundances of the metacercariae, in the mean size at age, and in the age composition for each shrimp species, demonstrating that separate shrimp populations existed. In some cases, natural boundaries separated populations of shrimp, for example, the island chain and shallow waters which lie between Imperial Eagle Channel and Trevor Channel. In other cases, such as occurred for the separate populations identified within Imperial Eagle Channel, there were no apparent topographic barriers. No evidence for the occurrence of offshore or onshore migrations of *P. jordani* or *P. dispar* was obtained.

Deux métacercaires digéniens, *Neolebouria tinkerbellae* et une espèce non identifiée (Metacercaria A), parasitant *Pandalus jordani*, et Metacercaria A parasitant *Pandalopsis dispar* ont été utilisés comme marqueurs biologiques naturels afin de déterminer le niveau d'isolement intraspécifique des populations. Des crevettes ont été prélevées dans les chenaux Imperial Eagle et Trevor, le détroit Barkley (côte ouest de l'île Vancouver, Colombie-Britannique) et dans une zone voisine située plus au large. La taille moyenne selon l'âge ainsi que la composition des âges de *P. jordani* et de *P. dispar* ont aussi été estimées. Un grand nombre de différences ont été notées entre les échantillons relativement à l'abondance des métacercaires, à la taille moyenne selon l'âge ainsi qu'à la composition des âges de chacune des espèces de crevettes, ce qui démontrait l'existence de populations isolées de crevettes. On a noté, dans certains cas, l'existence de limites naturelles entre les populations de crevettes, notamment le chapelet d'îles et les eaux peu profondes se trouvant entre les chenaux Imperial Eagle et Trevor. Dans d'autres cas, comme dans celui des populations isolées du chenal Imperial Eagle, il n'y avait aucune barrière topographique apparente. Les auteurs n'ont décelé aucun indice de migration vers la côte ou vers le large des populations de *P. jordani* et *P. dispar*.

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The use of naturally occurring parasites as biological markers or tags to determine population discreteness among marine and anadromous fishes has become an accepted methodology over the past 25–30 yr (Kabata 1963; Margolis 1963, 1982; MacKenzie 1983), but few attempts have been made to apply this technique to commercially important crustaceans (Owens 1985). The present paper reports on the results of one such study on exploited shrimp populations.

Three species of pandalid shrimp, *Pandalus jordani* Rathbun (smooth pink shrimp), *Pandalus platyceros* Brandt (prawn), and *Pandalopsis dispar* Rathbun (sidestripe shrimp), support commercial fisheries in Trevor Channel and Imperial Eagle Channel, Barkley Sound, west coast of Vancouver Island, British Columbia (Bernard 1982). However, these species are known to exist only in small quantities in Loudoun Channel, Barkley Sound (J. A. Boutillier, Pacific Biological Station, Nanaimo, B.C., pers. comm.). *Pandalus jordani* is also fished approximately 6–10 km offshore from Barkley Sound.

In the present study, five species of parasites were found in or on *P. jordani: Bopyroides hippolytes* (Krøyer) (Isopoda), Metacercaria A (Digenea), metacercariae of *Neolebouria tin-*

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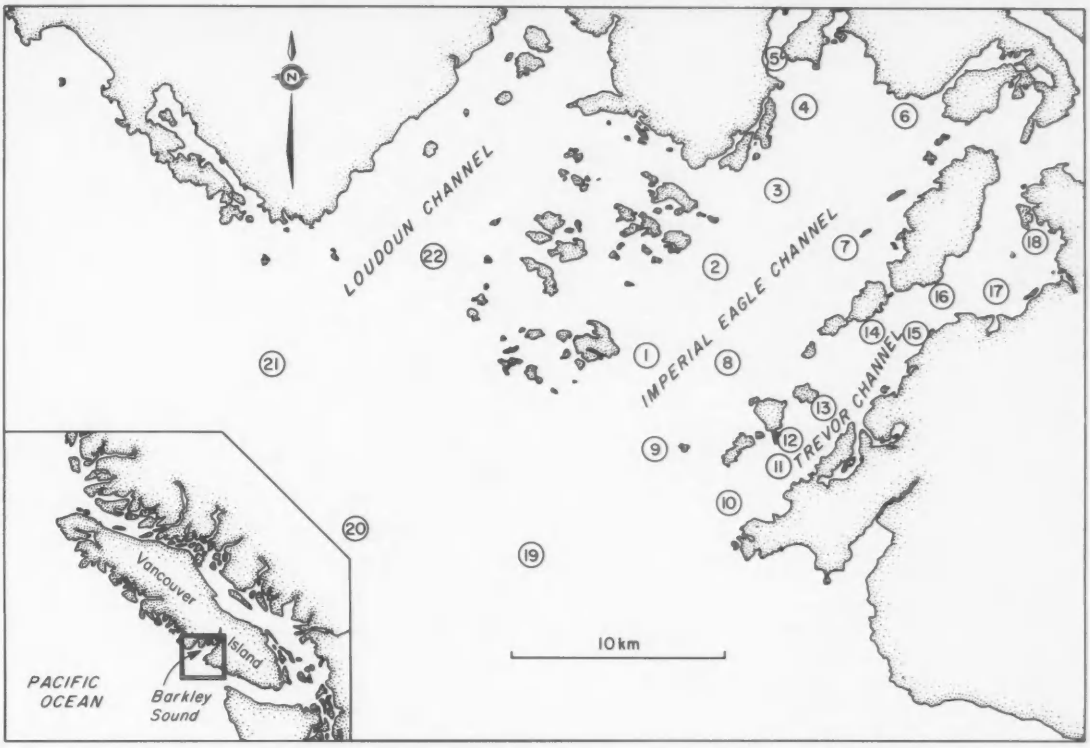

FIG. 1. Barkley Sound area showing sampling localities by tow number. Inset shows location of study area.

kerbellae Thompson and Margolis (Digenea), *Hysterothylacium* sp. larva (Nematoda), and *Thelohania* sp. (Microspora). Only two parasite species were found associated with *P. dispar: B. hippolytes* and Metacercaria A. No parasites were found in or on *P. platyceros*. Therefore, no further reference to this species will be made. The two species of digenean metacercariae proved useful as biological tags to study the mixing and movements of *P. jordani* and *P. dispar* within and among the above-mentioned areas.

MacKenzie (1983) listed six criteria for assessing the usefulness of a parasite species as a tag. Five that are relevant to the present study are as follows: (1) "The parasite should have significantly different levels of infection in the subject host in different parts of the study area." (2) "The method of examination should involve the minimum of dissection." (3) "The parasite should be easily detectable and identifiable." (4) "The parasite must have a life span, or remain in an identifiable form, in the subject host long enough to cover the time of the investigation." (5) "The parasite should have no marked pathological effects on the subject host."

The two species of metacercarial parasites used in this study satisfy these criteria. They are not damaged or dislodged by handling or freezing and are easily seen upon microscopic examination. The available evidence suggests that they have a long life span because their numbers increase with shrimp size, suggesting that they accumulate through time, and no dead or decaying metacercariae were ever observed. There is no evidence of pathological damage that would affect host survival or behaviour. The axiom for the parasite-tag method in relation to the present study is that if two samples from different localities contain shrimp with different parasite species or the same parasite species occurring at significantly different abundances, then shrimp are not completely mixing between the two localities. Unfortunately, the converse is not necessarily true because it is possible to have the same abundance of parasite species in two localities, even when shrimp are not mixing between these localities. The parasite method of stock discrimination also provides information on the likely absence of specific migratory movements. For example, if a parasite is abundant in one locality but absent or scarce in a second locality, then shrimp cannot be moving en masse from the first to the second locality; otherwise the parasite would be carried with the shrimp and appear in the second locality, provided the parasite has a sufficiently long life span. Again, the converse is not true and nothing can be said about the existence of a movement of shrimp from the second to the first locality.

J. A. Boutillier (pers. comm.) has noticed that *P. jordani* specimens of the same age-class were on average smaller in Trevor Channel than in Imperial Eagle Channel, which implies that *P. jordani* is not mixing between the channels. Therefore, the mean size of each age-class and the age composition of *P. jordani* and *P. dispar* were determined, interpreted with respect to shrimp movements and mixing, and the results compared with those obtained from parasite tags.

Materials and Methods

Shrimp were captured by towing a 13-m beam trawl along

TABLE 1. Abundance, intensity, mean intensity, and prevalence of metacercariae (based on untransformed data) by age-class of shrimp, all areas combined (see Materials and Methods for definitions of these statistics). Abundance, mean intensity, and prevalence are given as ranges (in parentheses) of values in individual samples preceded by means of all values. Intensity is given as a range of values in all samples combined.

Shrimp age-class	Abundance	Intensity	Mean intensity	Prevalence (%)
		Metacercaria A in Pandalopsis dispar		
1+	0.33 (0.03–0.86)	1–4	1.62 (1.00–2.00)	21 (3–52)
2+	0.71 (0.12–2.47)	1–14	2.53 (1.00–4.50)	30 (12–79)
3+	1.79 (0.21–2.91)	1–12	3.01 (1.33–3.90)	50 (16–91)
		Metacercaria A in Pandalus jordani		
1+	0.14 (0–0.27)	1–4	1.06 (1.00–1.67)	13 (0–25)
2+	0.69 (0.05–1.46)	1–18	2.13 (1.00–5.50)	32 (5–67)
3+	1.92 (0.31–3.16)	1–16	3.07 (1.25–4.13)	62 (23–86)
		Neolebouria tinkerbellae metacercaria in Pandalus jordani		
1+	0.02 (0–0.07)	1–2	1.08 (1.00–1.25)	2 (0–6)
2+	0.15 (0–1.33)	1–7	1.79 (1.00–4.00)	8 (0–33)
3+	0.19 (0–1.09)	1–5	1.56 (1.00–4.00)	12 (0–36)

the sea bed at 1.5 knots for approximately 30 min. Twenty-two tows were made from 14 to 20 June 1984 (Fig. 1); nine tows were from Imperial Eagle Channel (Tows 1–9), nine tows were from Trevor Channel (Tows 10–18), one tow was from Loudoun Channel (Tow 22), and three tows were from an area approximately 7 km offshore of Barkley Sound (hereafter referred to as the Offshore area (Tows 19–21)). Tows 10, 11, 12, and 22 were made at depths of 35–79 m. All other tows were made at depths of 80–137 m. The weight of *P. jordani* and *P. dispar* caught in each tow was recorded and expressed as kilograms per 30 min of towing.

Approximately 250 *P. jordani* from each tow in Imperial Eagle Channel and Offshore and from Tows 11, 13, 14, 15, and 18 in Trevor Channel, and 250 *P. dispar* from each of Tows 4 and 6 in Imperial Eagle Channel and Tows 16 and 17 in Trevor Channel, were taken randomly from the catch and frozen for length–frequency analyses. Additionally, approximately 100 *P. jordani* and 60 *P. dispar* were also selected from each tow to represent evenly all the sizes of shrimp caught and were frozen for parasitological examination.

Samples were thawed and the carapace length (Butler 1980) of each shrimp was measured to the nearest 0.1 mm. Schnute and Fournier's (1980) model was used to identify size-classes from the length–frequency data and provided an estimate of the mean, variance, and proportion of the total sample in each size-class. Only *P. jordani* of 13.0–24.0 mm and *P. dispar* of 17.0–32.9 mm inclusive were used for the parasitological examinations. The soft internal tissues of each shrimp were removed, squashed between glass slides (70 × 50 mm), examined using 6× magnification of a dissecting microscope, and the number of *N. tinkerbellae* and Metacercaria A counted.

The original metacercarial counts per shrimp were transformed by

$$(1)\quad Y_t = \log (Y + 1)$$

where Y and Y_t are, respectively, the original and transformed number of metacercariae per shrimp. The transformation helped normalize the data, increased homoscedasticity, and gave less weight to outlying points. Abundances, i.e. the mean number of each metacercaria per shrimp examined (Margolis et al. 1982), were calculated from the transformed metacercarial counts.

The *F*-test for coincidence of one or more straight lines was used to make statistical comparisons among Imperial Eagle Channel, Trevor Channel, and Offshore of the relationship of parasite abundance with shrimp size (Seber 1977). Visual intersample comparisons of the abundance of metacercariae were made by plotting the abundances (with 95% confidence limits) graphically (see Fig. 3 and 4). It can be shown, by using the *t*-test formula for the equality of two means, that there is an approximate probability of less than 0.005 that two samples were drawn from the same population when the 95% confidence limits of the means of two samples are not overlapping. The abundance of Metacercaria A in *P. jordani* was correlated with host size in 17 of 20 samples. Therefore, to remove the effect of shrimp size, the abundance of Metacercaria A in *P. jordani* was obtained from a least squares linear regression of transformed Metacercaria A counts per shrimp on shrimp size standardized to a *P. jordani* of 21 mm carapace length. The 95% confidence limits of the abundances were obtained from equation 7.5 of Seber (1977), but using equation 2 below to obtain the standard error instead of using the residual mean square from the *F*-test. This was done because the variance of the parasite abundance ($SD^2_{Y_t}$) was related to parasite abundance (Y_t) by

$$(2)\quad \log SD^2_{Y_t} = 0.91 \log \bar{Y}_t - 0.64.$$

The correlations between the abundance of *N. tinkerbellae* in *P. jordani* and carapace length, and the abundance of Metacercaria A in *P. dispar* and carapace length, were significant in only 4 of 20 and 2 of 10 samples, respectively. Therefore, standardization to a common carapace length was not required, and the mean and 95% confidence limits of the mean were calculated using conventional formulae.

The following definitions are provided for three other terms briefly mentioned in the Results section: prevalence = percent

infected with a given species of parasite in the sample examined; intensity of infection = the number of parasites of a given species, usually expressed as a range, found in individuals among the infected specimens in the sample examined; and mean intensity = mean number of parasites of a given species among the infected specimens in the sample examined (Margolis et al. 1982).

Results

Descriptions of Metacercarial Cysts

The two species of metacercariae have cysts differing in appearance and occupying different sites within the shrimp. The cyst of one species, *N. tinkerbellae*, was 0.216–0.510 mm in diameter with a translucent white cyst wall measuring approximately 0.03 mm in thickness and was found only in the heart muscle of *P. jordani*. A second species of metacercaria, which has not been identified and will be referred to subsequently as Metacercaria A, was found in the somatic musculature of the thorax and abdomen of *P. jordani* and *P. dispar*. The cysts of Metacercaria A had a thin translucent wall about 0.009 mm in thickness and were encapsulated in a thicker brown pigmented layer, presumably of host origin. The diameter of this cyst, including the pigmented layer, was 0.176–0.627 mm in *P. jordani* and 0.157–0.412 mm in *P. dispar*. Detailed descriptions of both species of metacercariae appear in Thompson and Margolis (1987).

Distribution of *P. jordani* and *P. dispar*

Pandalus jordani was abundant Offshore (Tows 19–21) and in the southwestern-most tow in Imperial Eagle Channel (Tow 9), where catches were 18.6–31.2 kg per 30-min tow, and common in the other tows in Imperial Eagle Channel and in seven of nine tows in Trevor Channel, where catches were 1.1–12.5 kg per 30-min tow. Small catches of *P. jordani* were recorded from Tow 16 in Trevor Channel and from Loudoun Channel (Tow 22) and none were caught in Tow 10 at the entrance to Trevor Channel.

Catches of 1.2–4.2 kg of *P. dispar* per 30-min tow were confined to Tows 2–6 in Imperial Eagle Channel and to Tows 15–18 in Trevor Channel. A small sample weighing 0.45 kg was obtained Offshore (Tows 20 and 21 combined) and was adequate for the determination of parasite abundance but not for length–frequency analysis. The remaining tows contained few (<0.1 kg) or no *P. dispar*.

Abundance, Intensity, Mean Intensity, and Prevalence of Metacercariae in Shrimp

The abundance, intensity, mean intensity, and prevalence of Metacercaria A in *P. dispar* and *P. jordani*, and of *N. tinkerbellae* in *P. jordani*, varied among samples and with age of the shrimp (Table 1). "Abundance" is used throughout the remainder of this paper for the determination of population discreteness, because it uses the combined information of the "mean intensity" and "prevalence" statistics.

For initial analysis of abundance data, samples were combined into three areas: Imperial Eagle Channel (Tows 1–9), Trevor Channel (Tows 10–18), and Offshore (Tows 19–21). Parasite counts were obtained for 859, 641, and 268 *P. jordani*, respectively, and 309, 289, and 51 *P. dispar*, respectively, for the above three areas.

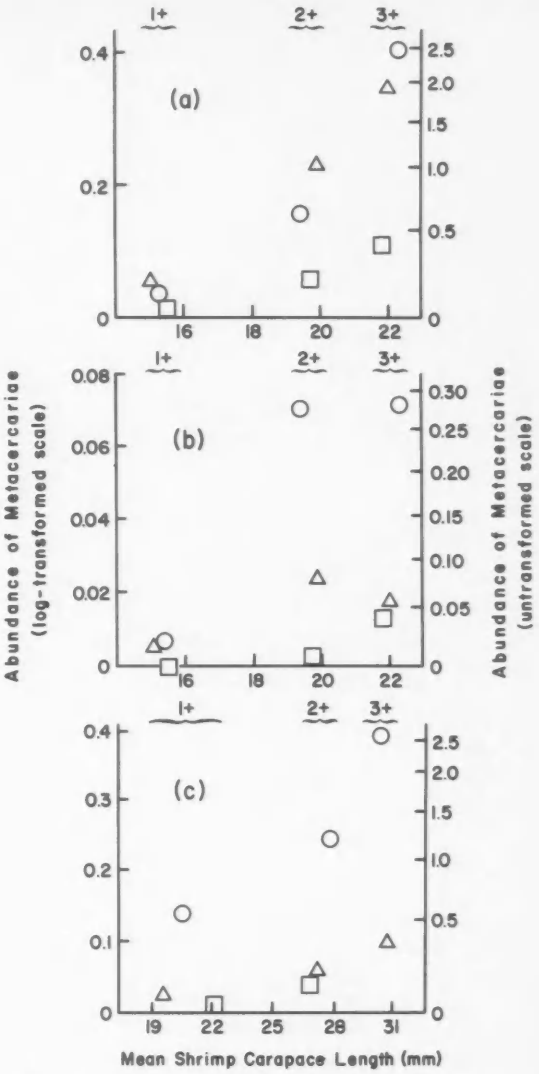

FIG. 2. Abundance of metacercariae in each age-class of shrimp sampled from Imperial Eagle Channel (○), Trevor Channel (△), and Offshore (□) for (a) Metacercaria A in *Pandalus jordani*, (b) *Neolebouria tinkerbellae* metacercaria in *Pandalus jordani*, and (c) Metacercaria A in *Pandalopsis dispar*. The untransformed scale is approximate because the points on this scale were recalculated from the transformed data using the formula given by Elliott (1971). The brackets group the points into age-classes. Note: no sample was obtained for the 3+ age-class of *P. dispar* from Offshore.

The abundances of Metacercaria A in *P. jordani* and *P. dispar*, and of *N. tinkerbellae* in *P. jordani*, were positively correlated with shrimp size, and therefore age, in Imperial Eagle Channel and Trevor Channel (Fig. 2). (The relationship between shrimp length and age is dealt with later.) In the Offshore area the abundance of Metacercaria A in *P. jordani* was also correlated with shrimp size, but no significant size correlations existed for Metacercaria A in *P. dispar* or for

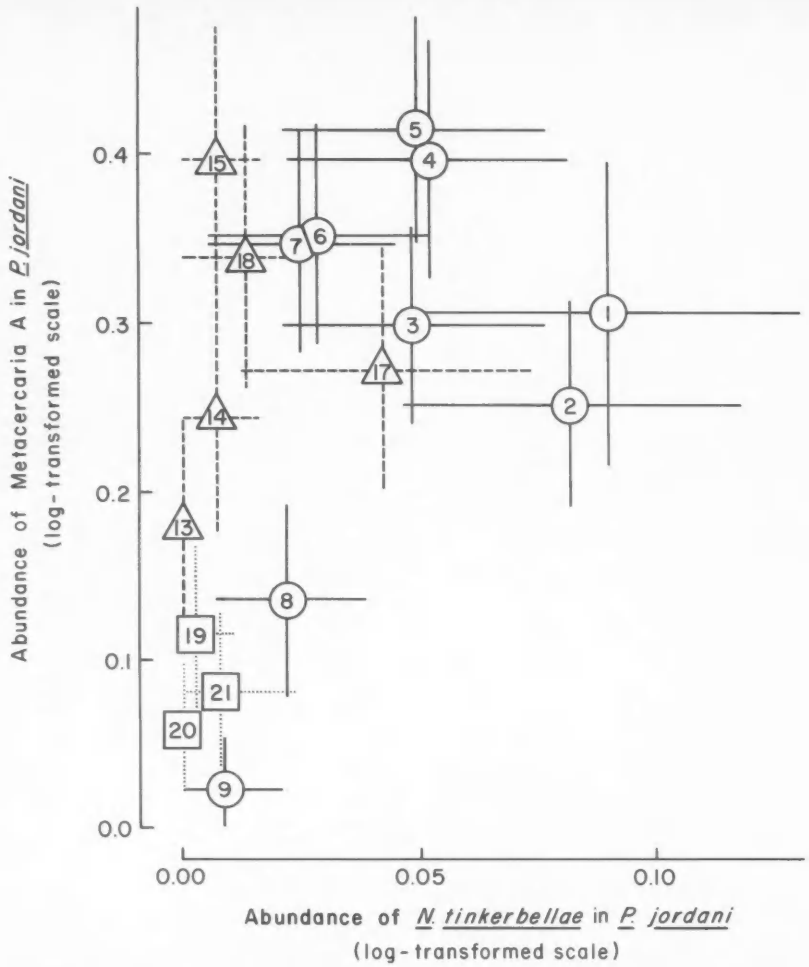

FIG. 3. Bivariate plot of log-transformed abundance data (and 95% confidence limits) of Metacercaria A and *Neolebouria tinkerbellae* metacercaria in *Pandalus jordani*. Sampling localities for Imperial Eagle Channel (○), Trevor Channel (△), and Offshore (□) are given by tow number within each symbol.

N. tinkerbellae in *P. jordani* ($r = 0.06$; df = 49; $P > 0.05$ and $r = 0.07$; df = 266; $P > 0.05$). The abundance of *N. tinkerbellae* in *P. jordani* was always lower than the abundance of Metacercaria A in *P. jordani* of equal size from the same area. No significant differences in the abundances of *N. tinkerbellae* occurred between the 2+ and 3+ age-classes of *P. jordani* from Imperial Eagle Channel or from Trevor Channel.

The abundance of Metacercaria A in *P. jordani* (Fig. 2a) in Trevor Channel was a little lower than that found in *P. jordani* of equal size in Imperial Eagle Channel ($F = 3.9$; df = 2, 1496; $P < 0.05$), but was much higher than found Offshore ($F = 56.5$; df = 2, 905; $P < 0.001$). Similarly, the abundance of *N. tinkerbellae* in *P. jordani* (Fig. 2b) of the same size from Trevor Channel was lower than that found in Imperial Eagle Channel ($F = 16.5$; df = 2, 1496; $P < 0.001$), although no significant differences in the abundance of this species occurred between Trevor Channel and Offshore ($F = 2.5$; df = 2, 905; $P > 0.05$). These differences in abundance of metacercariae in *P. jordani* were most noticeable in the 3+ age-class, with the differences being less obvious in the 2+ age-class, and virtually absent from the 1+ age-class.

A bivariate plot of the abundance of Metacercaria A against the abundance of *N. tinkerbellae* in *P. jordani* revealed samples with similar and different parasite abundances (Fig. 3). Tows 10–12, 16, and 22 were excluded from this analysis because there were insufficient large *P. jordani* in the samples to give reliable estimates of abundance. Samples of *P. jordani* from Trevor Channel (Tows 13–15, 17, and 18) and Offshore (Tows 19–21) form distinct clusters in Fig. 3. Imperial Eagle Channel has three distinct clusters corresponding to the geographical areas of northwestern Imperial Eagle Channel (Tows 1 and 2), eastern Imperial Eagle Channel (Tows 3–7), and southwestern Imperial Eagle Channel (Tows 8 and 9). The abundances of Metacercaria A and *N. tinkerbellae* in *P. jor-*

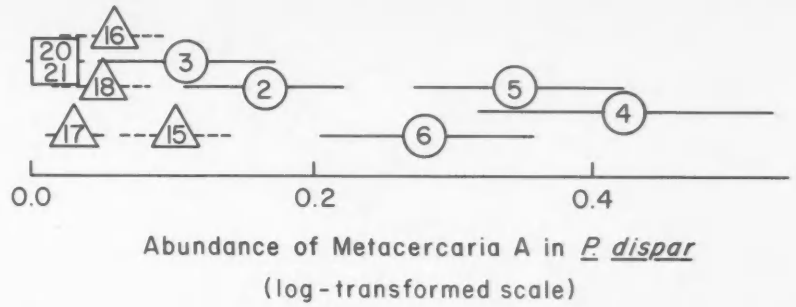

FIG. 4. Univariate plot of log-transformed abundance data (and 95% confidence limits) of Metacercaria A in *Pandalopsis dispar*. See Fig. 3 for explanation of symbols.

dani samples from eastern Imperial Eagle Channel were generally a little higher than found in Trevor Channel, although there was some overlap in the 95% confidence limits of some of the abundances. There was a comparatively high *N. tinkerbellae* abundance in *P. jordani* from northwestern Imperial Eagle Channel, indicating that the population of *P. jordani* in this subarea was distinct, and abundances of both species of metacercariae in *P. jordani* from southwestern Imperial Eagle Channel were low and were similar to *P. jordani* sampled Offshore (Fig. 3). There is limited evidence that *P. jordani* from Trevor Channel may be subdivided on the basis of the abundances of the two species of metacercariae. Tows 13, 15, and 17 are distinct, but Tows 14 and 18 are less readily distinguishable.

Differences in the abundance of Metacercaria A in *P. dispar* (Fig. 2c) of equal size sampled from different areas also existed. The abundances in Imperial Eagle Channel were several times greater than in Trevor Channel ($F = 60.5$; df = 2, 594; $P < 0.001$), but no significant differences existed between Trevor Channel and Offshore ($F = 1.7$; df = 2, 336; $P > 0.05$). This was observed for all age-classes of *P. dispar*.

A univariate plot of the abundance of Metacercaria A in *P. dispar* samples demonstrates certain intersample differences and similarities (Fig. 4). Imperial Eagle Channel samples are divided into two separate clusters consisting of Tows 4–6 and Tows 2 and 3. The abundance of Metacercaria A in *P. dispar* from Trevor Channel was slightly lower than that found in Tows 2 and 3 of Imperial Eagle Channel, and probably represents a distinct cluster. The absence of *P. dispar* from Tows 7, 8, and 14, however, indicates that *P. dispar* from Trevor Channel could not be confluent with *P. dispar* from the areas represented by Tows 2 and 3 in Imperial Eagle Channel. Metacercaria A in *P. dispar* was relatively rare Offshore but, as noted above, the abundance of Metacercaria A in *P. dispar* Offshore and in Trevor Channel was not significantly different.

Length–frequency and Age Composition of *P. jordani* and *P. dispar*

Three size-classes were identified in each of the length–frequency plots of 2368, 1140, and 742 individual *P. jordani* taken from Imperial Eagle Channel, Trevor Channel, and Offshore, respectively. The following discrete size-classes, 13.0–17.6, 17.7–21.0, and 21.1–24.0 mm carapace length, were obtained visually from a plot of the fitted model and corresponded to the 1+, 2+, and 3+ age-classes, respectively. These size-classes were used to separate shrimp into age-classes for the calculations of metacercarial abundance, intensity, mean intensity, and prevalence at age in Table 1 and Fig. 2. In reality, the size range for each age-class of shrimp overlaps and would be wider than given above. The 0+ age-class was not represented because of the small size of individuals in this age-class relative to the mesh size employed to collect the samples. A detailed inspection of the mean carapace lengths showed that specimens of *P. jordani* in each age-class were generally largest Offshore and smallest in Trevor Channel, with *P. jordani* from Imperial Eagle Channel being of intermediate size, indicating different growth rates among the areas (Table 2). No size differences occurred between 2+ age-class *P. jordani* in Imperial Eagle Channel and Trevor Channel ($t = 0.2$; df = 1043; $P > 0.05$), nor between 3+ age-class *P. jordani* in Imperial Eagle Channel and Offshore ($t = 0.4$; df = 526; $P > 0.05$).

TABLE 2. Length–frequency and age composition of *Pandalus jordani*.

	Age-class	Carapace length (mm) Mean	SE	Age composition (%)
Imperial Eagle Channel	1+	15.73	0.03	47
	2+	19.16	0.04	31
	3+	22.35	0.05	21
Trevor Channel	1+	15.24	0.04	59
	2+	19.15	0.05	26
	3+	21.80	0.07	15
Offshore	1+	16.22	0.05	86
	2+	19.91	0.10	11
	3+	22.39	0.12	3

The age composition also differed among the three areas. In Trevor Channel the younger age-classes were more common than in Imperial Eagle Channel, with this phenomenon being pronounced Offshore (Table 2). Catch-per-unit-effort data showed that the 1+ age-class Offshore was approximately 10 times more common than the 1+ age-class in Imperial Eagle Channel and Trevor Channel, whereas the 2+ and 3+ age-classes varied by less than a factor of 3 among the three areas (A. Thompson, unpubl. obs.).

The length–frequency analysis was performed on the 1440, 397, and 531 individuals obtained from the eastern, northwestern, and southwestern subareas of Imperial Eagle Chan-

TABLE 3. Length–frequency and age composition of *Pandalopsis dispar*.

	Age-class	Carapace length (mm) Mean	SE	Age composition (%)
Imperial Eagle Channel	1+	21.23	0.06	70
	2+	26.83	0.13	23
	3+	—[a]	—[a]	7
Trevor Channel	1+	19.61	0.08	67
	2+	26.43	0.13	30
	3+	—[a]	—[a]	3

[a]Inadequate numbers of individual *P. dispar* to produce reliable estimate of mean carapace length.

nel, respectively. Differences in the mean size of *P. jordani* for each age-class between the three subareas were small and probably not significant. The age composition of *P. jordani* in eastern Imperial Eagle Channel was uniform (34, 36, and 31% for the 1+, 2+, and 3+ age-classes, respectively); it was biased towards the 1+ age-class in northwestern Imperial Eagle Channel (60, 29, and 11% for the three respective age-classes), with the sample from southwestern Imperial Eagle Channel consisting mostly of the 1+ age-class (79, 21, and 0% for the three respective age-classes).

Peaks corresponding to the 1+, 2+, and 3+ age-classes were identified in length–frequency plots for the 462 and 337 *P. dispar* taken from Imperial Eagle Channel and Trevor Channel, respectively, for length–frequency analysis (Table 3). The approximate ranges in the carapace length for the three age-classes were 17.0–23.4, 23.5–28.9, and 29.0–32.9 mm. The 1+ and 2+ age-classes of *P. dispar* in Imperial Eagle Channel were significantly larger than the corresponding age–classes in Trevor Channel ($t = 15.7$; df = 544; $P < 0.01$ and $t = 2.1$; df = 208; $P < 0.05$, respectively), with the 3+ age-class being insufficiently represented to allow statistical comparisons.

The *P. dispar* age composition was similar in both channels, being biased in favour of the younger age-classes (Table 3).

Discussion

Pandalid shrimp are protandrous hermaphrodites with an initial planktonic phase in their life cycle lasting several months (Butler 1980). Their digenean parasites are the result of infections by cercariae released from molluscs and are, therefore, almost certainly acquired after settlement on the sea floor. Little is known about the movements of the planktonic stages, although their distribution is affected by ocean currents and winds (Rothlisberg 1975). Therefore, it is possible that shrimp larvae in Barkley Sound and Offshore may or may not mix. However, this study applies only to the postsettling history of *P. jordani* and *P. dispar*.

The differences in the relationship of metacercarial abundance with host size among samples and in the mean carapace length of each age-class showed that *P. jordani* formed separate populations in Imperial Eagle Channel, Trevor Channel, and Offshore and that *P. dispar* populations from Imperial Eagle Channel were distinct from *P. dispar* populations from Trevor Channel or Offshore. On the basis of available information, it is not possible to explain definitively why the parasite abundances differed according to locality, but the differences likely are related to differences in density and distribution of other hosts involved in the life cycles of the parasites.

Detailed examination of parasite abundances revealed that significant differences occurred among individual tows, and for *P. jordani* in Imperial Eagle Channel, these differences were used to produce subareas for analyzing length–frequency data. It should be remembered that the absence of significant differences in parasite abundances between two samples of shrimp is not evidence for complete mixing between the populations from which the samples were taken (see Introduction). Differences existed in the parasite abundances of *P. jordani* among the three subareas in Imperial Eagle Channel, and further differences were found in the age-class compositions to support the existence of three (or more) separate populations in this Channel. The similarities in parasite abundances and age compositions between southwestern Imperial Eagle Channel and Offshore *P. jordani* showed that in these areas a single population may exist. The high abundance of *N. tinkerbellae* in *P. jordani* from northwestern Imperial Eagle Channel showed that a distinct population exists there. Differences in the abundance of Metacercaria A and *N. tinkerbellae* in *P. jordani* also occurred within Trevor Channel, indicating that *P. jordani* was not mixing completely within this channel. However, it is not known whether mixing occurs among the three localities sampled Offshore because abundances of metacercariae in *P. jordani* from Tows 19–21 were similar. Differences in the abundances of Metacercaria A in *P. dispar* showed that there were at least two populations in Imperial Eagle Channel, although no distinct populations were identified in Trevor Channel, and *P. dispar* was too scarce Offshore to yield reliable parasite abundances.

The available evidence does not support the occurence of migrations of *P. jordani* en masse from Barkley Sound to the Offshore area. The occurrence of an offshore migration would have caused shrimp infected with metacercariae to be carried into the Offshore area, where they subsequently would have been detected in the samples. Metacercaria A and *N. tinkerbellae* were common in *P. jordani* from eastern and northwestern Imperial Eagle Channel, as was Metacercaria A in *P. jordani* from Trevor Channel, but both parasites were scarce Offshore and in southwestern Imperial Eagle Channel. Therefore, a large-scale offshore migration is unlikely to have occurred for *P. jordani* sampled during this study. An onshore migration of *P. jordani* would only serve to decrease the parasite abundances found in Barkley Sound, and this would be undetectable, since the metacercarial abundances of resident *P. jordani* in Barkley Sound would be unknown. For the same reason, it is not possible to use the length–frequency or age composition data to investigate the migration patterns, since the values for the resident populations would be unknown. Similar onshore and offshore migrations of *P. dispar* are not known to occur, since this species occurs almost exclusively in Barkley Sound and is uncommon Offshore.

The passages between the islands separating Imperial Eagle Channel from Trevor Channel are less than 20 m deep. Therefore, movements of *P. jordani* and *P. dispar* through these passages are unlikely, because neither shrimp species has been recorded at depths of less than 36 and 46 m, respectively (Butler 1980). A lack of mixing through the passages between these islands is confirmed by the parasite-tag data, because *P. jordani* from Trevor Channel (Tows 13 and 14) and Imperial Eagle Channel (Tows 7–9) have different parasite abundances (Fig. 3). Only very small quantities of *P. dispar* were caught

along the southern side of Imperial Eagle Channel, suggesting that limited or no mixing occurs through the passages between the islands separating Imperial Eagle Channel and Trevor Channel. Neither *P. jordani* nor *P. dispar* was found in the shallow entrance to Trevor Channel (Tow 10), which is less than 40 m deep. Therefore, movements into and out of Trevor Channel to Imperial Eagle Channel or Offshore, via its shallow entrance, are unlikely. The eastern passage between Imperial Eagle Channel and Trevor Channel is deeper than 98 m, and shrimp may pass through this passage. Loudoun Channel is less than 60 m deep and, as noted in the introduction, supports only small numbers of *P. jordani* and *P. dispar*. The small sample examined from this channel did not provide a basis for commenting on the existence or absence of migrations of these shrimp species into and out of Loudoun Channel.

This paper provides evidence for the existence of discrete populations of *P. jordani* and *P. dispar* among Imperial Eagle Channel, Trevor Channel, and the Offshore area. An exception to this was the southwestern subarea in Imperial Eagle Channel, which contained *P. jordani* with similar characteristics to those sampled Offshore. Topographical features, such as the islands between Imperial Eagle Channel and Trevor Channel, and the shallow entrance to Trevor Channel, formed natural barriers to postsettled populations of these shrimp species. However, discrete populations of *P. jordani* and *P. dispar* also existed, particularly within Imperial Eagle Channel, in the apparent absence of any natural barriers.

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Empirical Models for Zoobenthic Biomass in Lakes[1]

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Rasmussen, J. B., and J. Kalff. 1987. Empirical models for zoobenthic biomass in lakes. Can. J. Fish. Aquat. Sci. 44: 990–1001.

Estimates of macrozoobenthos from the literature were regressed against a series of limnological variables to yield empirical models for zoobenthic biomass in the profundal, sublittoral, and littoral zones of lakes. Variables indicative of phytoplankton biomass (chlorophyll concentration, total phosphorus concentration, and Secchi disk transparency) explained between 14 and 57% of the variance of zoobenthic biomass ($(g/m^2)^{0.1}$). Other factors such as humic colour, morphometry (slope, mean depth, ratio of mean to maximum depth, and lake area), and mean annual air temperature substantially increased the amount of explained variance. In the profundal and sublittoral zones, the best models explain 70% of the variance in zoobenthic biomass. Littoral zone models explained less than 50%, and this deficiency was attributed to sampling difficulties and to high local variability of slope and wave exposure in the littoral zone.

Les auteurs ont effectué des régressions entre des valeurs estimées du macrozoobenthos signalées dans les publications et une série de variables limnologiques afin d'obtenir des modèles empiriques de la biomasse du zoobenthos dans les zones profonde, sous-littorale et littorale des lacs. Les variables relatives à la biomasse phytoplanctonique (teneur en chlorophylle, concentration du phosphore total et transparence au disque de Secchi) expliquaient de 14 à 57 % de la variance de la biomasse zoobenthique ($(g/m^2)^{0.1}$). D'autres facteurs, notamment la couleur due aux matières humiques, la morphométrie (pente, profondeur moyenne, rapport entre la profondeur moyenne et la profondeur maximale, et superficie du lac) et la température annuelle moyenne de l'air, permettaient d'accroître de façon appréciable le pourcentage expliqué de la variance. Dans les zones profonde et sous-littorale, les meilleurs modèles permettaient d'expliquer 70 % de la variance de la biomasse zoobenthique. Les modèles de la zone littorale ne permettaient d'expliquer que moins de 50 % de la variance. Cette carence a été attribuée aux difficultés d'échantillonnage ainsi qu'à la variabilité locale élevée de la pente et au fait que la zone littorale est exposée à l'action des vagues.

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In lakes, the macrozoobenthos represents a major avenue of energy flow and an important source of food for the fish community (Eggers et al. 1978; Jónasson 1978; Wissmar and Wetzel 1978), and zoobenthic biomass can serve as a useful predictor of fish yield and biomass (Matuszek 1978; Hanson and Leggett 1982). Limnological factors that correlate with zoobenthic biomass should be important in fisheries science as predictors and/or control variables. Most previous attempts to explain variation in the abundance of zoobenthos have been based on variables related to lake trophic status (Kajak and Rybak 1966; Alley and Powers 1970; Jónasson 1972; Dermott et al. 1977; Brylinsky 1980; Rasmussen 1984; Hanson and Peters 1984), mean depth (Hayes 1957; Rawson 1955, 1960), or the morphoedaphic index (Johnson 1974).

Many of these studies dealt with only a single lake, but when many lakes were compared, less than half of the variance in zoobenthic biomass was accounted for. Yet, site-specific studies have suggested a considerable number of additional environmental factors, not related to trophic status, to be important correlates and/or determinants of zoobenthic biomass. Sediment particle size influences zoobenthic abundance (Mozley and Alley 1972; Nalepa and Thomas 1976; Cole and Weigmann 1983). Slope and, in the littoral zone, fetch affect sediment characteristics in lakes (Håkanson 1977; Duarte and Kalff 1986), and thus these easily estimated morphometric factors may explain some of the variance in zoobenthic biomass. Whitehouse (1971), Wiederholm (1971), Cole and Kelly (1978), and Rasmussen (1982) have shown increases in zoobenthic biomass in areas heated by thermal effluent. Carpenter (1983) and Fee (1979) provided evidence that lake basin shape (as estimated by the ratio of mean to maximum depth) affects phytoplankton production and sediment focusing, but the relationship of the depth ratio to zoobenthos has not been investigated. Similarly, the impact of dissolved humic matter on hypolimnetic oxygen availability and zoobenthic abundance and species composition was suggested by Thienemann (1925), Lundbeck (1926, 1936b), and Miyadi (1938) but the relationship was not quantified.

The purpose of our study was to relate, by linear regression analysis, zoobenthic biomass in lakes to those limnological parameters for which sufficient data could be found. The resulting models can then be used both to predict zoobenthic biomass under a wide range of limnological conditions and to identify those variables most promising for further investigation of functional relationships. Since limnologically important processes such as primary production, mixing, oxygen consumption, and sedimentation all differ greatly over depth gradients in lakes, the analyses were done separately for profundal

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TABLE 1. Sources of data used in regression analyses of zoobenthic biomass vs limnological parameters in a number of lakes.

Region and no. of Lakes	Zoobenthos estimate and source[a]	Other references
Canada, 29		
British Columbia, 8	Rawson 1934, 1939(SS); Larkin et al. 1950 (SS); Seather 1970 (S); Seather and McLean 1972 (S)	Rawson 1942; Janus and Vollenweider 1981
Alberta, 3	Rawson 1953a (IF); Rasmussen 1982 (A), 1984 (IF)	Nursall and Gallup 1971; Noton 1975
Saskatchewan, 6	Rawson 1959 (SS); Oliver 1960 (IF); Johnson 1971 (SS)	Rawson 1936
Manitoba, 1	Rawson 1948 (S)	
N.W.T., 5 (9 basins)	Rawson 1953b (S); Healey 1977 (S)	Rawson 1950; Fee et al. 1985
Ontario, 1	Rawson 1930 (IF)	Janus and Vollenweider 1981
Quebec, 1	Dermott et al. 1977 (IF); unpubl. data (IF)	Janus and Vollenweider 1981
United States, 27		
Minnesota, 1	Cole and Underhill 1965 (SS)	
Wisconsin, 2	Juday 1921, 1924a (IF)	Juday 1924b, 1942; Kozminski 1938
Indiana, 1	Scott et al. 1928 (IF)	Scott 1916, 1931
New York, St., 2	Harmon and Sohacki 1980 (IF)	Ogelsby 1978
Connecticut, 2	Deevey 1941 (SS)	Riley 1939
Maine, 18	Davis et al. 1978 (A)	
California, 1	Calhoun 1944 (S)	
Great Lakes, 5 + 3 bays	Alley and Powers 1970; Dermott 1984 (IF); Powers and Robertson 1965; Cook 1975 (S); Loveridge and Cook 1976 (S); Shivastava 1974 (S)	Nalepa and Quigley 1983; Janus and Vollenweider 1981
Europe, 62		
Norway, 1	Vik 1978 (A)	Kloster 1978; Larsson et al. 1978
Sweden, 4	Grimås 1949 (IF); Grimås et al. 1972 (A); Wiederholm 1971 (A)	
Finland, 3 (13 basins)	Särrkä and Paasivirta 1972 (IF); Kansaren and Aho 1981 (IF); Jumppanen (1976); Bagge and Jumppanen 1968	Valovirta 1959; Särrkä 1972, 1979, 1983
Iceland, 1	Jónasson 1979 (A)	
Denmark, 1	Jónasson 1972, 1978 (A)	Ryding 1980
Northern Germany, 19	Lundbeck 1926 (SS)	Thienemann 1920, 1925, 1928; Ohle 1934a, 1934b, 1940; Hutchinson 1957
Central Germany, 1	Frank 1982 (IF)	
Alps, 14	Lundbeck 1936a, 1936b (SS); Bretschki 1975 (A)	Haempel 1930; Ruttner 1937; Pesta 1929; Ruttner 1937; Pechlaner 1966
Poland, 5	Żytkowicz 1976 (A); Kentzer 1980 (A); Kajak and Dusoge 1975a, 1975b, 1976	Adamczak et al. 1979; Rybak 1972; Kajak 1978, 1983; Zdanowski 1983; Zdanowski et al. 1984
USSR, Karelia, 2	Zhadin and Gerd 1961 (IF?)	Winberg 1980
Japan, 2 (3 basins)	Yamagushi and Fukuhara 1971 (A); Iwakuma and Yasuno 1981 (A)	Aizaki et al. 1981; Miyadi 1938
New Zealand, 2	Timms 1980 (A)	

[a]SS = spring–summer mean; S = summer mean; IF = ice-free season mean; A = annual mean.

(PZB), sublittoral (SZB), and littoral zoobenthic (LZB) communities.

Methods

All estimates of zoobenthic biomass in lakes that could be coupled with limnological data collected within 10 yr of the study date were used (Table 1). The zoobenthic biomass estimates normally represent the ice-free season mean values for a depth stratum or individual station within a lake. No attempt was made to be restrictive, and consequently, averages range from means obtained from one or two sampling dates to annual means collected over 1 or more yr. Samples were taken either with Ekman–Birge, Shipek, or Ponar grabs, or with corers of various types, and sieved through screens with apertures ranging from 0.2 to 0.8 mm. Most studies reported biomass of animals preserved in formalin (5 or 10%) or ethanol (70–90%) (grams wet weight per square metre). Those estimates expressed as dry weight were converted by dividing by 0.15, or by the specific conversion factor reported for the particular study. As most authors exclude large pelecypods (unionids) from their estimates, we did the same for the studies that included them.

Zoobenthos estimates from below the thermocline were considered profundal, estimates from depths supporting macrophytes or macroalgae were called littoral, and those from beyond the littoral, but above the thermocline were classed as sublittoral. A few studies did not provide sufficient information to make these distinctions, and for these cases the maximum depth of plant colonization was estimated from the empirical model of Chambers and Kalff (1985), and the maximum mixing depth was estimated from lake area using the model of Arai (1981).

The most widely available indicators of phytoplankton biomass were Secchi disk transparency and the concentration of chlorophyll *a* (micrograms per litre). For benthos estimates

that could not be associated with a chlorophyll measurement, this variable was estimated from the following equation:

(1) Chlorophyll ($\ln(\mu g/L)$) = 6.383 − 1.481 transparency ($\ln$ (m)) − 1.504 colour (mg Pt/L + 25)$^{0.25}$ + 0.0571 conductivity ($\mu S)^{0.5}$ R^2 = 0.86, SE of estimate = 0.40, RMS = 0.016, N = 147

which was constructed from data on 147 nonsaline (conductivity < 1000 μS) lakes (Riley 1939; Armstrong and Schindler 1971; Schindler 1971; Patalas 1971; Grimås et al. 1972; Davis et al. 1978; Bloomfield 1978; Särrkä 1979; Ryding 1980; Aizaki et al. 1981; Janus and Vollenweider 1981; Costella et al. 1983).

The salinity was expressed as conductivity (microsiemens per centimetre, 25°C). When only total dissolved solids (milligrams or milliequivalents per litre) were reported, the conductivity was estimated using published conversion relationships (Hutchinson 1957; Rodhe 1949). Most lakes had conductivities between 20 and 1000 μS. We did not include the relatively few saline lakes with conductivities several orders of magnitude higher than this because of their limnological peculiarities, especially the extremely high hypolimnetic oxygen deficits that occur even in lakes with low phytoplankton biomass (Melack 1983; Zhadin and Gerd 1961).

Following Juday and Birge (1933), most North American authors have used the Hazen colour standard (milligrams platinum per litre) as an estimator of humic material. In Europe, colour has been measured with several methods, including the methyl orange (Ohle 1934a, 1934b) and the Forel–Ule methods (Thienemann 1925; Hutchinson 1957). In addition, direct measurements of dissolved organic matter (Juday and Birge 1932; Åberg and Rhode 1942) and chemical oxygen demand using $KMnO_4$ (Thunmark 1937; Juday and Birge 1932; Zhadin and Gerd 1961) were also found. All of these methods can be interrelated with reasonable precision, and consequently, Hazen colour was estimated from other measures using Eq. 2 and 3 (Juday and Birge 1932; Thunmark 1937; Åberg and Rodhe 1942) and eq. 4 (Thienemann 1920, 1925, 1928; Ohle 1934a, 1934b, 1940; James and Birge 1938; Riley 1939; Åberg and Rodhe 1942; Hutchinson 1957):

(2) Colour (mg Pt/L + 25)$^{0.5}$ = 4.12 + 0.479 dissolved organic carbon (mg/L) R^2 = 0.92, SE of estimate = 0.747, RMS = 0.558, N = 55

(3) Colour (mg Pt/L + 25)$^{0.5}$ = 4.173 + 0.464 $KMnO_4$ oxygen demand (mg/L) R^2 = 0.93, SE of estimate = 0.735, RMS = 0.540, N = 48

(4) Colour (mg Pt/L + 25)$^{0.5}$ = −0.725 + 0.235 Forel–Ule colour R^2 = 0.91, SE of estimate = 0.326, RMS = 0.106, N = 28.

The transformation used for colour ((mg Pt/L + 25)$^{0.5}$) was necessary to produce good fit and homoscedasticity.

Mean depth, area, the ratio of mean to maximum depth, and slope were used as morphometric factors. Slope was approximated either from bathymetric maps or hypsographic curves. There were not nearly enough estimates of sediment particle size to include this variable itself in the analysis. However, the relationship between slope and sediment coarseness (Håkanson 1977; Duarte and Kalff 1986) appears to be sufficiently general to permit slope to act as an adequate surrogate. Whenever zoobenthos estimates were characteristic of a distinct basin within a lake, the morphometric data used were those characterizing the basin rather than the whole lake.

Neither mean temperature – depth relations nor heat budgets were available for the majority of lakes. Water temperature is, however, well predicted from mean annual air temperatures together with lake area and mean depth (Arai 1981). The temperature variable used, therefore, was mean annual air temperature obtained from climatic atlases (U.S. Department of Environmental Sciences Administration 1968; Steinhauser 1970; Parkins 1974; Fisheries and Environment Canada 1978).

Regression Procedures

Zoobenthic biomass was transformed to the tenth root, since this produced good linear fit between predicted and observed biomass ($(g/m^2)^{0.1}$), in addition to homoscedasticity of residuals for all models tested. The logarithmic transformation used by Hanson and Peters (1984) in all cases overtransformed the biomass data leading to a significant negative correlation between the absolute value of the residual and the predicted log biomass. The transformations used for the regressor variables were selected for their ability to remove dependence of residuals on the given regressor variable (improve fit) rather than their ability to maximize R^2. Ratios and proportions are often transformed by either probit or arc-sine transformations (Sokal and Rohlf 1982) to normalize extreme values. For slope, the range was from 20 to 0.01%, and since no high values were present, the logarithmic transformation provided better fit. It was not necessary to transform the depth ratio, since all values were between 0.2 and 0.7 (Sokal and Rohlf 1982).

Zoobenthic biomass ($(g/m^2)^{0.1}$) was first regressed separately against four trophic indicator variables (chlorophyll *a* concentration ($(\mu g/L)^{0.5}$), chlorophyll *a* estimated from Eq. 1 (backtransformed after Miller 1984), total phosphorus concentration ($\ln(\mu g/L)$), and transparency (meters)) for the profundal, sublittoral, and littoral zones. To facilitate comparison between these trophic variables, this comparison was performed only on the benthos estimates for which data on all four trophic variables were available. Second power terms were only tested when residuals were found to be correlated with the regressor variable, and neither exponential nor logarithmic transformation could correct this. Thus for chlorophyll, the best fit was provided by the parabolic regression on $(\mu g/L)^{0.5}$ and its second power (μg/L). Due to the collinearity produced by such power terms, their significance was tested by a combined significance test (SYSTAT III) in addition to the partial F = 4.0 criterion of the multiple regression procedure (Belsley et al. 1980). For total phosphorus the logarithmic transformation provided the best fit, and for transparency the untransformed variable was most effective.

The ability of trophic variables alone to predict PZB, SZB, and LZB (tenth roots) was then compared to that of multiple regression models produced by the backward stepwise selection procedure (partial F = 4.0 was the criterion for variable entry and leaving). This was carried out both on the data set that contained estimates of all of the trophic variables and on the complete data set for each. Each model tested contained one of the trophic variables (chlorophyll, total phosphorus, or transparency) in addition to the following: colour ((mg Pt/L + 25)$^{0.5}$, pH, mean depth ($\ln$ (m)), sampling depth ($\ln$ (M)), lake area ($\ln$ (km^2)), slope ($\ln$ %), ratio of mean to maximum depth, mean annual temperature (°C), conductivity ($(\mu S^{0.5})$), as well as a number of methodological variables. These included

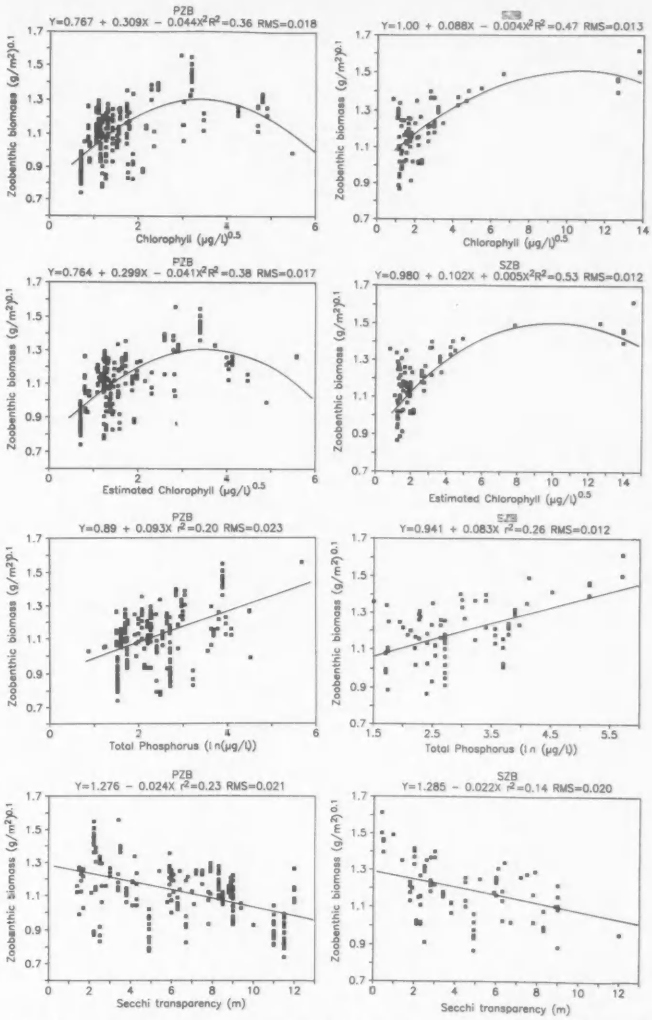

FIG. 1. Relationship between zoobenthic biomass (PZB and SZB) and four variables indicative of phytoplankton biomass. This analysis was confined to zoobenthic biomass estimates for which data for all four of the trophic indicators was available. The fitted regression equations are above each graph (Y is the variable on the ordinate and X is the variable on the abscissa). Estimated chlorophyll refers to chlorophyll estimated from Eq. 1.

the type of bottom sampler (large Ekman, small Ekman, Ponar, or corer), chlorophyll estimation method (spectrophotometric method, or estimation from Eq. 1), colour estimation method (chloroplatinate method, Eq. 2, 3, or 4), type of benthos estimate (annual, ice-free season, or summer means), and the type of preservative used (formalin or ethanol). One dummy variable (01) was entered per category. Residuals were also tested (post hoc) for dependence on interactions between dummy variables and predicted biomass. Although the regressors were not independent of each other, all pairwise correlations were 0.5 or less. The diagnostic criteria outlined by Belsley et al. (1980, in SYSTAT III), including the condition index (>30) and the variance decomposition (one variable contributing >0.5 of the variance for two or more regression coefficients), failed to reveal any serious multicollinearities. The collinearity between the power terms of chlorophyll was dealt with in the same manner as outlined above for the trophic variable regressions.

The explained variance (R^2) was partitioned into component contributions from different variables by path analysis using equations outlined by Li (1975) and Sokal and Rohlf (1982). The component coefficients (d^2) from direct paths are $b'^2(b'$ are the standardized partial regression coefficients) and for indirect (collinear) paths between variables i and j are $2b_i'b_j'r_{ij}$ (r_{ij} is the correlation coefficient between variables i and j). Thus, for the variables i and j the combined $d^2 = b_j'^2 + b_j'^2\,2b_i'$

TABLE 2. Comparison of the power of four trophic variables to predict zoobenthic biomass ($(g/m^2)^{0.1}$) in single variable and multiple regression.[a]

	Trophic variable	Best single variable model (Fig. 1) R^2	RMS	Best multiple regression R^2	RMS
Profundal (N = 213)[b]	Chlorophyll ($(\mu g/L)^{0.5}$)	0.36	0.018	0.74	0.0072
	Chlorophyll estimated from Eq. 1	0.38	0.017	0.73	0.0079
	Total phosphorus (ln ($\mu g/L$))	0.20	0.023	0.63	0.0104
	Transparency (m)	0.23	0.021	0.70	0.0083
Sublittoral (N = 87)[b]	Chlorophyll ($(\mu g/L)^{0.5}$)	0.47	0.013	0.74	0.0056
	Chlorophyll estimated from Eq. 1	0.53	0.012	0.74	0.0057
	Total phosphorus (ln ($\mu g/L$))	0.26	0.018	0.72	0.0061
	Transparency (m)	0.14	0.020	0.73	0.0059
Littoral (N = 42)[b]	None of the trophic parameters were significantly related to LZB in either the single variable or multiple regressions for this data set.				

[a]The single trophic variable models are parabolic regressions when the x^2 term makes a significant contribution. The retention criterion for variables in all models was $p < 0.05$.
[b]These analyses were restricted to zoobenthos estimates for which all four trophic variables were available.

$b_j' r_{ij}$. The two power terms of chlorophyll were combined in this fashion to yield the combined d^2 for the chlorophyll parabola. The d^2 for the remaining variables that had no strong and obvious pairwise collinearities were simply b'^2. Since the coefficient of multiple determination (R^2) is the sum of direct and indirect determinations, the magnitude of the difference $R^2 - \Sigma^i d_i^2$ will reflect the contribution from the remaining collinear paths. The sign of this difference can be negative, since in multiple regression $\Sigma^i b_i'^2$ can be >1, and the coefficients for collinear paths can be negative (Li 1975).

Lakes Excluded from the Analysis

Although data from 131 lakes were used to build the regression models, there were some lakes, which for reasons apparent at the outset, would have to be treated separately. These included saline and/or meromictic lakes (Lake Werowrap (Walker 1973; Paterson and Walker 1974), Lenore and Soap lakes (Lauer 1959; Anderson 1958), Pyramid Lake (Galat et al. 1981)), the lakes of great antiquity with their distinct endemic faunas (Lake Baikal (Koshov 1963), Lake Ohrid (Stanković 1960), and Lake Biwa (Horie 1984)), and the large, but shallow and turbid, wind-stressed lakes with continually disturbed sediment (Neusiedlersee (Löffler 1979), Balaton Lake (Ponyi et al. 1983), and Tjeukemeer (Beattie 1982)). The number of zoobenthic biomass estimates from tropical lakes was insufficient to justify their inclusion (Lake Sibaya (Allanson 1979) and Lake Chad (Carmouze et al. (1983)). However, data from all of the excluded lakes were compared with the extrapolated predictions made from the regression models.

Results

Relationship of Zoobenthic Biomass to Trophic Variables

Four trophic variables (Fig. 1; Table 2) were tested for their ability to explain variance in PZB, SZB, and LZB using data sets for which all four variables could be provided. The best single variable regression explained only 38% of the variance in PZB and 57% in SZB, and none were significant predictors of LZB for this data set. Parabolic regressions for both measured chlorophyll and chlorophyll estimated from Eq. 1 were the best predictors in both the profundal and the sublittoral zones for both the trophic variable models and the multiple regressions that included all significant predictors (Table 2). The parabolic regressions (Fig.1) predict maximum PZB at a chlorophyll concentration of 11 $\mu g/L$ and a sharp decline in PZB above this level. For SZB, near-maximum biomass is associated with chlorophyll concentration in the 30–200 $\mu g/L$ range, and no sharp decline occurs at high concentrations. Transparency was not a good predictor in the single variable model but performed nearly as well as chlorophyll in the multiple regression (Table 2). Both the single variable and the multiple regressions based on total phosphorus (ln ($\mu g/L$)) explained less variance in both PZB and SZB than did those based on chlorophyll. The multiple regressions (PZB and SZB) derived from this data set (Table 2) were very similar to those obtained for the complete data sets (Table 3) and are therefore not presented.

Multiple Regression Models (Table 3; Fig. 2).

The multiple regressions derived from the complete set of predictors explained substantially more variance and had much smaller residuals than the models based solely on trophic variables (Tables 2 and 3). The best models obtained for PZB (Eq. 5), SZB (Eq. 9), and LZB (Eq. 12) all contained chlorophyll as the trophic variable. In addition to providing the highest R^2 and smallest residuals, the chlorophyll-based models were also the least influenced by collinearities ($R^2 - \Sigma d^2$, Table 3). These models also contained significant contributions (negative) from colour and slope. The effect of lake area (negative) was highly significant above the thermocline (SZB and LZB) but not in the profundal zone. Mean depth and sampling depth made significant contributions (negative) only in the profundal zone, and the depth ratio and mean annual air temperature were significant (positive) in the profundal and sublittoral zones but not in the littoral zone. None of the methodological variables were significant in any of the models.

The multiple regressions based on total phosphorus as the trophic variable (Eq. 6 and 10) had lower R^2, larger residuals,

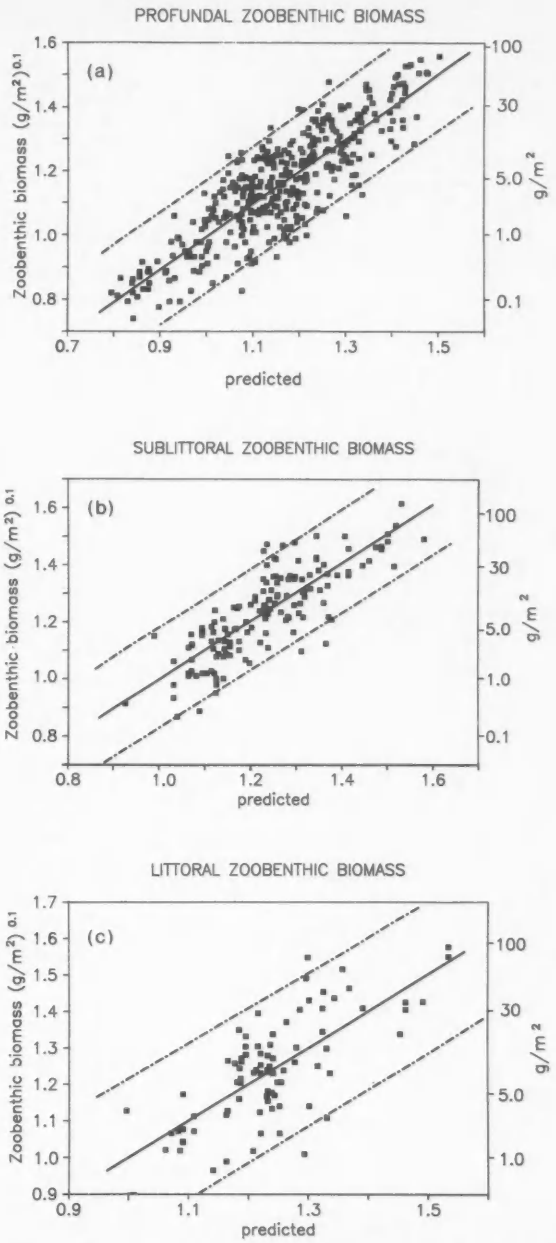

FIG. 2. Fit of zoobenthic biomass (transformed to 0.1 power) to multiple regression models given in Table 3 showing 95% confidence limits (broken lines). (a) $PZB^{0.1}$ predicted from Eq. 5; (b) $SZB^{0.1}$ from Eq. 9; (c) $LZB^{0.1}$ from Eq. 12. The right-hand axes denote untransformed zoobenthic biomass.

and were more influenced by collinearity than those based on chlorophyll (Tables 2 and 3). The models based on transparency (Eq. 7, 11, and 13) explained nearly as much variance and had only slightly larger residuals than those based on chlorophyll. The models based on transparency had a significant contribution from conductivity (positive), and in addition, collinearity involving transparency, colour, and conductivity contributed strongly to the variance of zoobenthic biomass in these models. This is consistent with the relationship shown by Eq. 1. The trophic variable used did not greatly affect on the regression coefficients obtained for colour and the morphometric variables (Table 3). The regression models obtained for the littoral zone explained far less variance and had much larger residuals and fewer significant variables than those obtained for the sublittoral or profundal zone. Table 4 lists the variables used in each data set and gives their ranges and median values.

Discussion

Most previous attempts to explain variation in the abundance of the benthos have emphasized the role of phytoplankton biomass (Kajak and Rybak 1966; Jónasson 1972; Dermott et al. 1977; Brylinsky 1980; Rasmussen 1984; Hanson and Peters 1984). Our analysis clearly supports the importance of this effect in all three depth zones as indicated by the significance of the chlorophyll *a* concentration, the total phosphorus concentration, or the Secchi transparency. The parabolic relationship obtained for zoobenthos versus chlorophyll in the profundal zone (Fig. 1) suggests that when phytoplankton biomass is high, the effect of its decomposition on the hypolimnial oxygen concentration becomes substantial. The regression coefficient for the negative second power chlorophyll term is much stronger in the profundal zone than above the thermocline (Table 3). Brylinsky (1980) also found that hypolimnial oxygen concentration had a significant effect on profundal zoomacrobenthic production.

Hanson and Peters (1984) accounted for less than half of the variance in mean profundal macrozoobenthos biomass using the total phosphorus concentration of the surface water. We also found that our estimators of lake trophic status (chlorophyll, total phosphorus, or transparency) explained much less than half of the variance in profundal biomass, but that the highly significant contributions from several variables unrelated to trophic status (colour, slope, depth ratio, and mean annual air temperature) made the total variance explained with our models substantially higher than the best models reported by Hanson and Peters (1984). Table 5 outlines a comparison of the fit obtained by our Eq. 8 and Eq. 6 from Hanson and Peters (1984) to estimates of MPZB for a set (n = 61) of lakes for which all predictors required by both models could be obtained. Since different transformations for MPZB were used (Eq. 8 uses $MPZB^{0.1}$ and Hanson and Peters used $\log_{10}$ MPZB), predictions from both models were therefore back-transformed (correcting for bias) and subtracted from observed (untransformed) MPZB estimates. Table 5 clearly shows that our model provides the better fit, but this is not completely convincing due to the strong heteroscedasticity of the untransformed residuals. Therefore, the predictions from both models were transformed to both tenth root and $\log_{10}$ and subtracted from similarly transformed MPZB estimates, and in both transformations, our model gives significantly smaller residuals. There is, however, a substantial amount of overlap between the MPZB estimates used to make this comparison and those used to develop both models. We are therefore preparing a completely independent data set in order to compare the predictive power of the two models.

TABLE 3. Multiple regression analysis of profundal (PZB), mean profundal (MPZB), subittoral (SZB), and littoral (LZB) zoobenthic biomass. Dependent variable: (a) models test chlorophyll as the trophic variable, (B) models, total phosphorus, and (c) models test transparency. — = not

Predictors	$PZB^{0.1}$ (a), Eq. 5	$PZB^{0.1}$ (b), Eq. 6	$PZB^{0.1}$ (c), Eq. 7	$MPZB^{0.1}$ (a), Eq. 8
Intercept	1.35731***	1.57987***	1.82497***	1.19160***
Chlorophyll $((\mu g/L)^{0.5})$	0.28835 } (0.37)***	—	—	0.28764 } (0.36)***
Chlorophyll $(\mu g/L)$	−0.04349 }	—	—	−0.04485 }
Total phosphorus (ln $(\mu g/L)$)	—	0.06066 (0.12)***	—	—
Secchi transparency (m)	—	—	−0.02022 (0.14)***	—
Conductivity $(\mu S/cm)^{0.5}$	n.s.	n.s.	0.00726 (0.02)***	n.s.
Sampling depth (ln (m))	−0.05755 (0.07)***	−0.05243 (0.06)***	−0.06338 (0.08)***	—
Mean depth (ln (m))	−0.02287 (0.02)**	−0.03672 (0.04)**	−0.02959 (0.03)***	−0.05562 (0.08)***
Lake area (ln (km^2))	n.s.	n.s.	n.s.	n.s.
Slope (ln %)	−0.03203 (0.07)***	−0.0441 (0.12)***	−0.03123 (0.06)***	−0.02990 (0.05)***
Mean/max. depth	0.28386 (0.04)***	0.30521 (0.05)***	0.27853 (0.04)***	0.34539 (0.05)***
Colour $((mg\ Pt/L + 25)^{0.5})$	−0.06779 (0.11)***	−0.07301 (0.12)***	−0.07886 (0.14)***	−0.05928 (0.11)***
Temperature (°C)	0.00405 (0.02)***	0.0040 (0.02)***	0.00547 (0.03)***	0.00602 (0.03)***
R^2 (Adjusted for df)	0.72	0.65	0.69	0.70
SE of estimate	0.090	0.100	0.093	0.082
Residual mean square	0.0081	0.010	0.0086	0.007
$R^2 - \Sigma d^2$	0.02	0.12	0.16	0.02
N	384	218	383	105

*Chlorophyll estimation technique (spectrophotometric measurement vs. estimation from Eq. 1), PZB (213 vs. 177), MPZB (61 vs. 44), SZB variables were never significant.

The three variables colour, slope, and mean annual air temperature were all highly significant despite the crudeness of many of the estimates used. The colour estimates were derived from a number of indices (see methods), and slope estimates are averages for depth zones derived from bathymetric maps, or sometimes approximations from hypsographic curves, and rarely correspond to the slope at the exact sites sampled. Air temperatures are only loosely correlated with water temperature (Arai 1981). Thus, it is likely that when these variables are measured more precisely, and at the exact sampling sites, much better models of macrozoobenthos will result.

Regression analysis is an effective method of revealing patterns of relationship between variables in complex data sets, and in addition to its predictive applications, when combined with the method of path analysis (Li 1975; Sokal and Rohlf 1982), it can serve as the basis for hypotheses about functional relationships (Draper and Smith 1981). Since collinearities do not contribute appreciably to the variance of zoobenthic biomass in our chlorophyll-based models, we do not hesitate to speculate about mechanisms that might be involved in the relationships we have demonstrated. However, these should not be interpreted as inferences or conclusions, but as hypotheses intended to stimulate further study of functional relationships.

The effects of colour may represent direct inhibitory effects of humic substances which are known to occur in some invertebrates (Petersen et al. 1986), or alternatively, they may result from the effects of the chemical oxygen demand of these substances on redox conditions in sediments or bottom waters (Juday and Birge 1932).

The decline in zoobenthic biomass with increasing slope is probably the result of a reduced ability of steep slopes to retain fine sedimenting materials, and the relationship between slope and sediment particle size (Håkanson 1977; Duarte and Kalff 1986) supports this interpretation. In the littoral zone, Duarte and Kalff (1986) found a strong negative relationship between the biomass of rooted submerged macrophytes and slope, and this would likely also contribute to the effects of slope on zoobenthos, since macrophytes enhance zoobenthic biomass (Rasmussen 1982; Davies 1982). Wind fetch is known to be a major determinant of wave height and the disturbance regime at the sediment–water interface (Smith and Sinclair 1972). Therefore, if retention of fine surficial sediments were important, one would expect that wind fetch (as reflected by lake area in these models) would have a significant negative effect on zoobenthic biomass in the littoral and sublittoral (but not in the profundal zone), and this is what our models show.

The positive effect of mean annual air temperature on biomass may result from positive temperature effects on either bacterial activity in sediment or on the rates of resource processing by animals. This effect could also be the result of reduced winter ice cover (both time and thickness of ice cover) in reducing the effects of stagnation.

The effect of the ratio of mean to maximum depth on profundal and sublittoral biomass is highly significant, but in the opposite direction to that proposed by Fee (1979) and Carpenter (1983) for phytoplankton biomass. Since lakes with high ratios of mean to maximum depth have generally accumulated a considerable quantity of sediment (Hutchinson 1957), and lakes in granitic watersheds (lowest sediment production (Slaymaker 1982)) have the lowest depth ratios, it is reasonable to propose that the effect of depth ratio on zoobenthos biomass probably involves the accumulation and focusing of sediment and/or detritus in some way. Mozley and Alley (1972) found zoobenthos to be more abundant in samples from fine, soft sediments than in coarser sediments, and this finding is consistent with the observed effects of depth ratio and slope in the present study.

Table entries are regression coefficients (coefficient of determination (d^2)) and probability levels $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$). entered; n.s. = not significant but tested.

$SZB^{0.1}$ (a), Eq. 9	$SZB^{0.1}$ (b), Eq. 10	$SZB^{0.1}$ (a), Eq. 11	$LZB^{0.1}$ (a), Eq. 12	$LZB^{0.1}$ (c), Eq. 13
1.27299***	1.25982***	1.43429***	1.38527***	1.53115***
0.07472 } (0.24)***	—	—	0.10392 (0.28)***	—
−0.00435 }	—	—	n.s.	—
—	0.04409 (0.07)***	—	—	—
—	—	−0.01882 (0.10)***	—	−0.01495 (0.08)**
n.s.	n.s.	0.00565 (0.01)**	n.s.	0.00975 (0.03)**
n.s.	n.s.	n.s.	n.s.	n.s.
n.s.	n.s.	n.s.	n.s.	n.s.
−0.01384 (0.10)***	−0.01932 (0.13)***	−0.01114 (0.06)***	−0.01001 (0.04)*	−0.01582 (0.09)***
−0.02512 (0.06)***	−0.03556 (0.10)***	−0.02202 (0.04)***	−0.01850 (0.03)*	−0.03299 (0.10)**
0.25725 (0.05)***	0.32848 (0.06)***	0.31289 (0.08)***	n.s.	n.s.
−0.04098 (0.11)***	−0.03793 (0.06)***	−0.04958 (0.14)***	−0.04985 (0.12)***	−0.04686 (0.11)**
0.00334 (0.02)*	n.s.	0.00362 (0.02)*	n.s.	n.s.
0.70	0.72	0.69	0.48	0.47
0.080	0.078	0.084	0.106	0.106
0.0064	0.0061	0.0071	0.0112	0.0112
0.12	0.30	0.24	0.01	0.07
155	87	155	84	84

(87 vs. 68), and LZB 42 vs. 42). Dummy variables (see methods) testing the effect of chlorophyll estimation technique and other methodological

TABLE 4. Ranges and median values of variables used in regression analyses for PZB, SZB, and LZB (Table 3). Table entries are (minimum−maximum) median values.

Variable	PZB (Eq. 5−8)	SZB (Eq. 9−11)	LZB (Eq. 12−13)
Zoobenthic biomass (g/m^2)	(0.5−90) 4.5	(0.24−120) 7.9	(0.30−95) 8.6
Chlorophyll (μg/L)	(0.5−30) 2.4	(0.5−190) 5.1	(0.7−30) 4
Total phosphorus (μg/L)	(4−390) 15	(4−390) 18	(4−85) 11
Transparency (m)	(0.8−12) 5	(0.4−12) 3.4	(1.2−12) 5
Conductivity (μS)	(21−780) 222	(29−870) 277	(29−870) 300
pH	(5.9−9.2) 7.4	(5.4−8.6) 7.7	(6.0−9.1) 7.5
Colour (mg Pt/L)	(0−85) 8	(0−188) 10	(0−70) 8
Sampling depth (m)	(7−330) 29	(2.0−20) 8.0	(0.5−12) 3.0
Mean depth (m)	(4−199) 14	(1.1−199) 12.1	(2−199) 15
Lake area (km^2)	(0.03−82 367) 24	(0.03−82 367) 12.5	(0.3−82 367) 20
Mean/max. depth	(0.2−0.68) 0.39	(0.2−0.71) 0.36	(0.2−0.67) 0.36
Slope (%)	(0.001−16) 1.8	(0.01−20) 1.5	(0.01−20) 2.3
Mean annual air temperature (°C)	(−8−+13) 6	(−8−+13) 6	(−8−+13) 6
Screen size (mm)	(0.2−0.8) 0.4	(0.2−0.8) 0.4	(0.2−0.7) 0.5

The variables used in this analysis were chosen because they were available for a large number of lakes and were reasonable proxies for variables that we hypothesized would influence zoobenthic biomass. In addition, they can be easily estimated (often from maps) for predictive purposes. Although we suggest improved measurement of these variables to facilitate better prediction, attention should also be drawn to other variables that could be used in functional analyses to shed more light on mechanisms involved. Measurements of dissolved oxygen, dissolved organic matter, and E_h profiles at the sediment−water interface (and/or interstitial water) could permit more direct analysis of stagnation, and perhaps, colour effects. If slope and lake area actually affect benthos through their effects on retention of fine food-rich sediment, then perhaps measurements of sediment particle size, water content, organic matter content, sediment bacteria, and net sedimentation in combination with the wave height−depth relationship could produce more direct relationships to benthos than those we observed for morphometric predictors. Studies of the fate and transport of allochthonous sediment and detritus at stream mouths, and the fate of macrophyte detritus originating in weed beds, could also shed light on how morphometric variables, including the depth ratio, affect zoobenthos.

Our analyses show that the major hindrance to the development of precise whole-lake models of macrozoobenthic biomass lies in the large residual mean square associated with the littoral biomass models. The probable reason for this is that littoral estimates in the literature generally do not represent total biomass, but rather a variable fraction of this, since they were obtained with grabs (Ekman−Birge and Ponar). These

TABLE 5. Comparison of the ability of Eq. 6 (Hanson and Peters 1984)[a] and Eq. 8 (this study) to predict mean profundal zoobenthic biomass (MPB) (N = 61).

	(a) mean $\lvert Y - \hat{Y}^* \rvert$ ± SE[b]	(b) mean $\lvert Y^{0.1} - \hat{Y}^{0.1} \rvert$ ± SE[b]	(c) mean $\lvert \log_{10} Y - \log_{10} \hat{Y} \rvert$ ± SE[b]
A. Eq. 6	9.32±2.30	0.107±0.010	0.418±0.045
B. Eq. 8	3.34±0.58	0.073±0.0064	0.285±0.026
t	2.5	2.86	2.56
p	<0.02	<0.005	<0.02

[a]Eq. 6: $\log_{10}$ MPB = 0.742 $\log_{10}$ total phosphorus (µg/L) − 0.090 $\log_{10}$ area (km^2).
[b]$\hat{Y}$ = MPB predicted from models A and B corrected for backtransformation bias after Miller (1984).

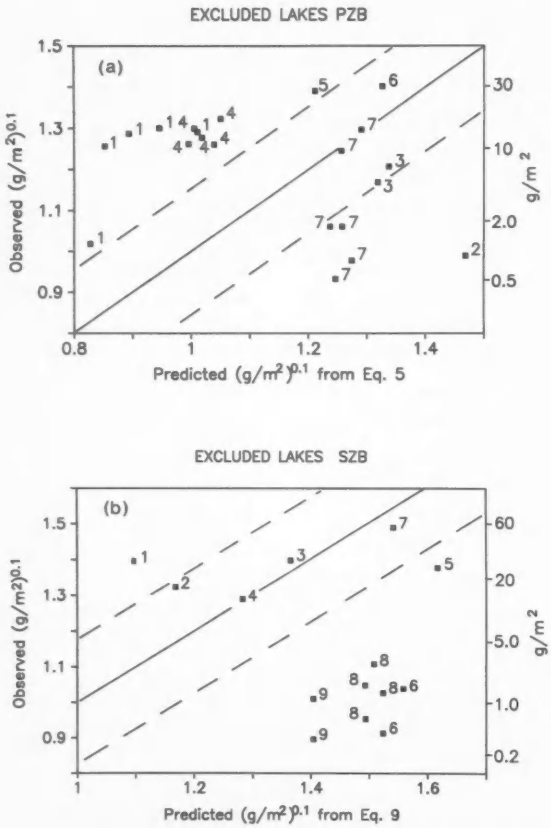

FIG. 3. Comparison of zoobenthic biomass estimates from excluded lakes with predictions from multiple regression models. Solid lines represent predicted = observed and broken lines represent 95% confidence limits. The right-hand axes denote untransformed zoobenthic biomass. (a) From Eq. 5; profundal zoobenthos: 1 = Lake Baikal (endemic), 2 = Lake Kinneret (anoxic), 3 = Lake Sibaya (tropical), 4 = Lake Ohrid (endemic), 5 = Lake Biwa, 6 = Soap Lake (saline), 7 = Pyramid Lake (saline; for this lake, biomass estimates were formulated from densities using species-specific mean weights). (b) From Eq. 9; sublittoral zoobenthos: 1 = Lake Baikal (endemic), 2 = Lake Ohrid (endemic), 3 = Lake Lenore (saline), 4 = Pyramid Lake (saline), 5 = Lake Chad (tropical, wind-stressed), 6 = Neusiedlersee (wind-stressed), 7 = Lake Werowrap (saline), 8 = Tjeukemeer (wind-stressed), 9 = Lake Balaton (wind-stressed).

are ineffective on the sometimes compact littoral sediments and do not quantitatively sample macrophytes. The explanatory power of the regression models obtained for LZB probably reflect this methodological deficiency, with the best relationship accounting for only 49% of the variance (Table 3). Many authors avoided sampling the littoral zone, probably due to the methodological difficulties and the extreme local variability in habitat conditions (Downing and Cyr 1985); therefore, the number of estimates available for the littoral zone is much lower than for the sublittoral and profundal zones. Lastly, the difficulty of relating the benthos estimates to average morphometric conditions was probably another factor contributing to the low explanatory power of the littoral zone models. By relating site-specific measurements of environmental factors to total LZB estimates obtained by combining core samples taken by SCUBA with a specific sampling procedure for epiphytic benthos (Downing 1986), it is possible to develop models for LZB that have substantially more predictive power than the literature-based models (J. B. Rasmussen, in prep.).

Zoobenthos Biomass from Lakes Excluded from the Analyses

Biomass estimates were available for three ancient lakes whose fauna is composed largely of endemic taxa, Lake Baikal (Koshov 1963; Zhadin and Gerd 1961; Moskalenko 1972), Lake Biwa (Horie 1984), and Lake Ohrid (Stanković 1960). Profundal biomass from all three greatly exceeded (Fig. 3a) values predicted from Eq. 5. Sublittoral values from Lake Baikal and Lake Ohrid did not exceed predicted values by nearly as much (Fig. 3b). This is consistent with the fact that the shallow water fauna of these lakes has fewer endemic taxa than the profundal fauna. Unfortunately, none of these lakes excluded from the regression models had enough data from their littoral zones to make comparisons possible. The data points for upper profundal and sublittoral biomass from saline lakes fell within the 95% confidence limits of the freshwater lake models (Fig. 3). At depths >30 m in Pyramid Lake the profundal biomass was much lower than expected, and this was associated with hypoxic conditions (Galat et al. 1981), a feature typical of the hypolimnia of deep saline lakes (Melack 1983), even those with extremely low plankton biomass. In Lake Kinneret (only moderately saline, but eutrophic) the hypolimnion is completely anoxic for much of the year (Sernuya 1978), and PZB was far below the value predicted from Eq. 5 (Fig. 3a). Similarly, the zoomacrobenthos from shallow, wind-stressed turbid lakes was far below that predicted from Eq. 9. The wind-stressed turbid lakes are very shallow, but the

poor light penetration virtually eliminates the littoral zone. Consequently, the whole lake can be considered as sublittoral habitat. Herzig (1979) found that these shallow turbid lakes contained much higher zooplankton biomass than expected on the basis of their phytoplankton biomass. Resuspension of fine particles from the sediment–water interface may be adversely affecting zoobenthos, but may be beneficial in some way to zooplankton.

In summary, this study of published data yielded empirical models relating macrozoobenthic biomass, in the profundal, sublittoral, and littoral zones of lakes, to a series of limnological parameters. The biomass of zoobenthos was linked, although very loosely, to indices of lake trophic status, and the amount of explained variance was greatly enhanced by a number of variables not related to water column productivity (including humic colour, slope, depth ratio, and lake area). Therefore, macrozoobenthic biomass is an aspect of lake richness that cannot be adequately represented by water column trophic indices alone. The study also points to the need for improved measurement of variables such as colour, slope, and wave exposure, and more detailed studies of their relationship to zoobenthos, in order to more fully explore their potential in limnology as predictors and control variables.

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Equilibrium Models for Seasonal Dynamics of Plankton Biomass in Four Oligotrophic Lakes

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Walters, C. J., E. Krause, W. E. Neill, and T. G. Northcote. 1987. Equilibrium models for seasonal dynamics of plankton biomass in four oligotrophic lakes. Can. J. Fish. Aquat. Sci. 44: 1002–1017.

Plankton biomass dynamics were monitored over an 11-yr period in four coastal British Columbia lakes while they were disturbed by salmonid introductions, fertilization, and zooplankton harvesting. Except for dramatic zooplankton responses to fertilization, the lakes had relatively simple and stable seasonal biomass patterns, with midsummer zooplankton peaks and no clear seasonal cycles in biomass of unicellular phytoplankton. Simple models predict that equilibrium biomasses should follow the observed pattern, provided zooplankton grazing and metabolic rates are temperature independent; experimental measurements of these rates did not show clear temperature dependence. Enclosure studies showed that phytoplankton biomass can return quickly (48–72 h) to equilibrium after disturbance, but zooplankton biomass responds more slowly (2- to 3-wk recovery times), yet fast enough to track a seasonally varying equilibrium. We conclude that the biomass equilibrium of unicellular phytoplankton is set by grazing and metabolic rates of zooplankton, while the zooplankton biomass equilibrium is set by phytoplankton productivity.

La dynamique de la biomasse planctonique a été étudiée pendant 11 ans dans quatre lacs côtiers de la Colombie-Britannique pendant la période où ceux-ci faisaient l'objet de repeuplements en salmonidés, de fertilisation et de récolte du zooplancton. Sauf pour des réactions marquées du zooplancton face à la fertilisation, les lacs montraient des régimes relativement simples et stables de la biomasse saisonnière : des pics du zooplancton à la mi-été et aucun cycle saisonnier précis de la biomasse du phytoplancton unicellulaire. Des modèles simples prédisent que les biomasses d'équilibre devraient suivre le régime observé si le broutage par le zooplancton et les taux métaboliques sont indépendants de la température; des quantifications expérimentales de ces taux n'ont pas révélé une dépendance évidente vis-à-vis de la température. Des études en bassin ont révélé que la biomasse phytoplanctonique peut rapidement revenir à l'équilibre (48–72 h) après des perturbations mais que la biomasse zooplanctonique réagit plus lentement (temps de récupération allant de 2 à 3 semaines) quoique cette réaction soit assez rapide pour suivre la variabilité saisonnière de l'équilibre. Les auteurs formulent la conclusion que la biomasse d'équilibre du phytoplancton unicellulaire est déterminée par les taux de métabolisme et de broutage du zooplancton tandis que la biomasse d'équilibre du zooplancton est fixée par la productivité phytoplanctonique.

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Temperate plankton communities are usually viewed as highly variable systems, with seasonal changes occurring so rapidly as to preclude the temporary establishment of any equilibrium or balance of production and loss rates. This view has arisen mainly from the study of species populations, for which it certainly appears to be valid. However, it is possible that more aggregate measures, such as total phytoplankton and zooplankton biomasses, may follow simpler patterns that are predictable from general models that consider only major rate processes such as primary production and zooplankton filtering. The limited success of biomass compartment models at fitting field data supports this possibility (Scavia and Robertson 1979; Walters et al. 1980; Fedra et al. 1981), as does the growing literature on empirical relationships among aggregate variables measured across collections of lakes (Dillon and Rigler 1974; Brylinsky 1980; Prepas and Trew 1983; Hanson and Peters 1984; Stockner and Shortreed 1985; McQueen et al. 1986). Recently, the debate about complexity of behavior has been focussed by Carpenter and Kitchell (1984), who use a size-structured plankton model to argue that large changes in primary production can arise from population interactions; a counter argument predicting simple behavior was presented by O'Neill and Giddings (1979) and by several authors in Halfon (1979).

This paper develops simple theoretical models that predict how phytoplankton and zooplankton biomasses should vary seasonally in oligotrophic lakes if the biomasses remain near moving equilibria defined by environmental factors that affect primary production rates, but are not influenced by invertebrate and vertebrate predation. We then compare the model predictions with data from an 11-yr field study on four oligotrophic British Columbia coastal lakes (Fig. 1; Table 1). We monitored plankton populations in these lakes in some detail over the period 1973–83 and conducted various disturbance experiments for which the theoretical predictions might fail. Three lakes were initially barren of fish because of barriers to dispersal; cutthroat trout (*Salmo clarki clarki*) were introduced deliberately into Eunice Lake in 1974–75 and accidentally (barrier failure) into Gwendoline Lake around 1978–79, and Dolly Varden char (*Salvelinus malma*) were introduced into

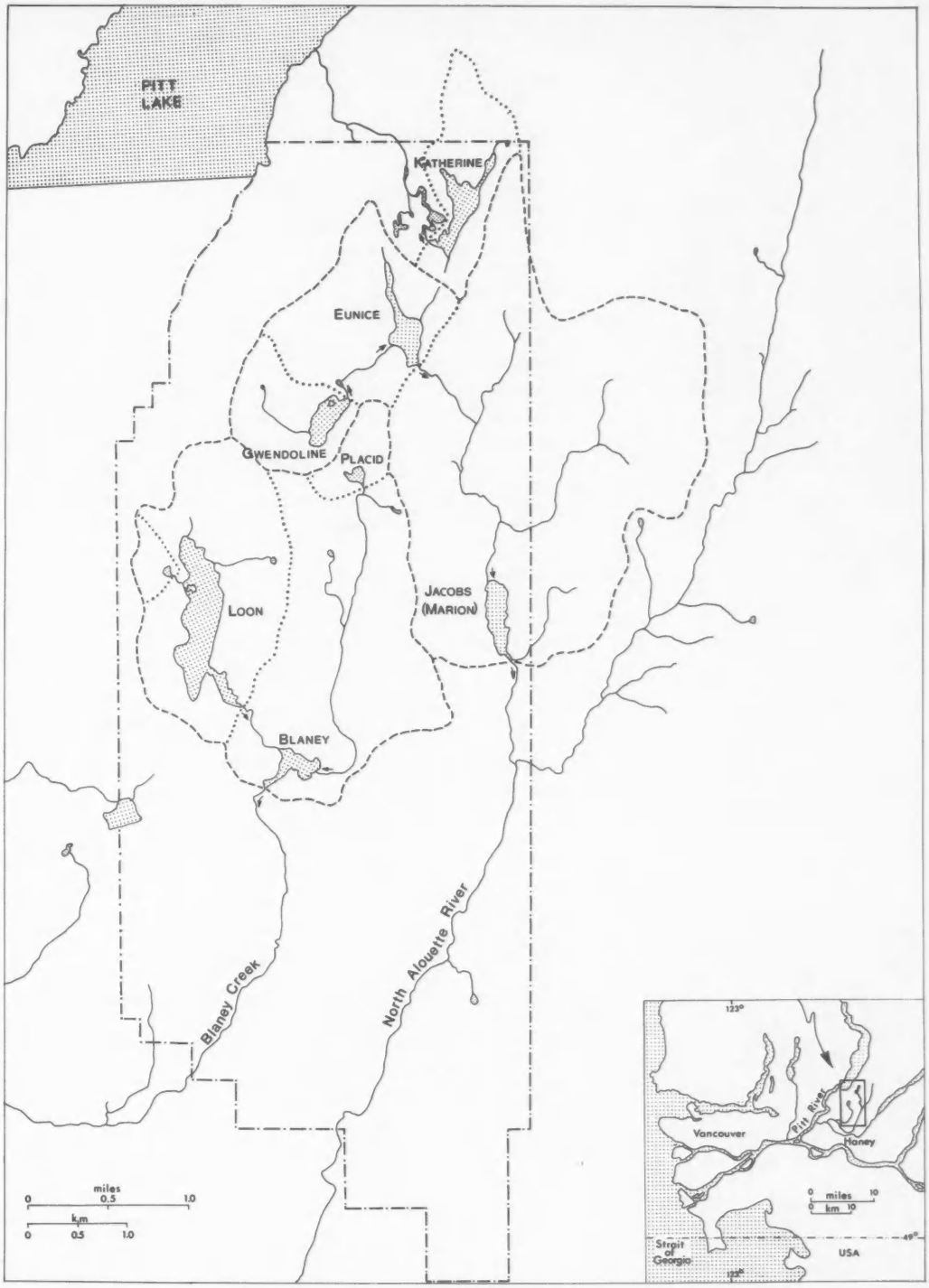

FIG. 1. Location of study lakes in the University of British Columbia Research Forest. (From Northcote and Clarotto 1975.)

TABLE 1. Some physical–chemical characteristics of the Research Forest study lakes. (From Northcote and Clarotto 1975.)

Characteristics of lakes	Katherine	Gwendoline	Eunice	Placid
Elevation (m)	505	522	480	510
Drainage area (ha)	108	81	191	44
Surface area (ha)	20.7	13.0	18.2	1.6
Maximum depth (m)	29	27	42	7
Mean depth (m)	7.5	13.4	15.8	4.3
Total dissolved solids (mg/L)	15	18	16	17–23
pH	6.6	6.6	6.4	5.5–6.6
Color (Pt units)	10–15	15	15	20–25
Transparency (Secchi disc, m)	6.5–9	5–7.2	6–10	4–4.5
Epilimnion depth, late summer (m)	6	5	4–6	4
Hypolimnion O_2 minimum (mg/L)	3.6	4.0	0.6	~1

Katherine Lake in 1974–1975 (Northcote et al. 1978; Hume and Northcote 1985). Placid Lake had an established cutthroat trout population, and we attempted to disturb its plankton community during two periods in 1979–80 by taking 50% weekly harvests of large zooplankton (>0.5 mm) with a large (5 × 2 m mouth) tow net (Krause 1984). Gwendoline Lake was fertilized in May–August 1979 by weekly additions of 0.2 g inorganic fertilizer (N:P = 15:1 by weight)/m^2 applied as NH_4NO_3 and NH_4PO_4. Besides these crude field disturbances, various bag, enclosure, and laboratory experiments have been conducted to test particular hypotheses about community structure (Neill 1978, 1981a, 1981b, 1984, 1985; Neill and Peacock 1980; Peacock 1982; Peacock and Smyly 1983; Olenick 1983; Bowerman 1983) and provide estimates of key rates such as zooplankton filtering (Buckingham 1978; Krause 1984). None of our experiments were designed to deliberately test the models presented here; the models arose in hindsight as we attempted to explain some of the observed patterns.

Theoretical Predictions

This section develops three simple models for phytoplankton and zooplankton biomass dynamics and derives several qualitative predictions from these models. The motivation for the models was the predator–prey theory of Rosensweig and MacArthur (1963), Smith (1969), and Lane and Levins (1977). We attempted to explicitly avoid multicompartment representation of phenomena such as nutrient cycling. Earlier experience with multicompartment models (Walters et al. 1980) led to similar qualitative predictions as we present quantitatively here, at least for oligotrophic lakes where the phytoplankton community is not dominated by large, ungrazable algal forms. For all three models, we shall assume that phytoplankton biomass (P) and zooplankton biomass (Z) interact according to the rate structure

$$(1)\quad dP/dt = \alpha_t P - F_t PZ$$

$$(2)\quad dZ/dt = F_t Pz - M_t Z$$

where the specific rates α_t, F_t, and M_t may in principle depend on P and Z as well as on time-varying environmental conditions; α_t is the net rate of algal biomass growth per unit biomass in the absence of grazing (net primary production rate less mortality and sinking rates), F_t is the zooplankton filtering rate per unit zooplankton biomass, and M_t is the total zooplankton loss rate per unit biomass (excretion plus metabolism plus mortality).

The simplest possible model for a seasonal system using eq. (1) and (2) is to assume that α, F, and M depend only on environmental factors such as light and temperature, so that $\alpha_t = a_t$, $F_t = f_t$, and $M_t = m_t$ where a_t, f_t, and m_t are seasonal functions of time calculated from the environmental factors. In this case, the time-varying equilbrium phytoplankton and zooplankton biomasses $\bar{P}_t$ and $\bar{Z}_t$ are given simply by setting $dP/dt = 0$ and $dZ/dt = 0$ in eq. (1) and (2):

Model 1:

$$(3)\quad \bar{P}_t = m_t/f_t$$

$$(4)\quad \bar{Z}_t = a_t/f_t.$$

A striking feature of eq. (3) is that equilibrium phytoplankton biomass is predicted to depend only on the zooplankton rates m and f; this prediction follows from the assumption that M_t and F_t are not influenced by zooplankton biomass, so that Z always builds up (or falls) to the level where $f_t PZ = m_t Z$ at which the P is just dense enough for grazing intake to balance zooplankton losses. This conclusion is robust to more complex assumptions about the dependence of M_t and F_t on P; for example, both are likely to be decreasing functions of P. Note further from eq. (4) that zooplankton biomass is predicted to be proportional to phytoplankton growth rate, a_t if the filtering rate f_t remains relatively constant. Finally, note that eq. (3) and (4) predict no seasonality in $\bar{P}$ and $\bar{Z}$ at all if the three rates m_t, f_t, and a_t are all exactly proportional to a single environmental factor such as temperature. Unfortunately, model 1 has a serious flaw: it predicts neutrally stable cycles around $\bar{P}$ and $\bar{Z}$, with no limit on the amplitude of such cycles due to factors such as free nutrient exhaustion at high biomass levels.

As a second, more realistic model, we suppose that phytoplankton growth rate α_t is proportional to the free concentration N_t of some limiting nutrient for which (1) the total concentration T does not change seasonally and (2) there is not significant binding or absorption into biomass pools other than P and Z, so that

$$(5)\quad T = N_t + n_P P_t + n_Z Z_t$$

where n_P and n_Z are nutrient contents per unit phytoplankton and zooplankton biomass, respectively. If α_t is proportion to N_t, then $\alpha_t = a_t(T - n_P P_t - n_Z Z_t)$ where a_t is now the specific algal growth rate per unit nutrient available and is assumed to vary over time in relation to environmental variables such as light and temperature. Substituting this model for α_t into eq. (1) and (2), and again assuming that f_t and m_t are independent of P and Z, we get the equilibrium predictions:

Model 2:

$$(6)\quad \bar{P}_t = m_t/f_t$$

$$(7)\quad \bar{Z}_t = a_t(T - n_P m_t/f_t)/(f_t + a_t n_Z).$$

Surprisingly, the predicted phytoplankton equilibrium for this model is the same as for model 1; again the basic argument is that any increase in phytoplankton productivity (through variation in a_t or T) will be transmitted into an increase in Z until P is driven down to the concentration where $f_t PZ = m_t Z$. However, model 2 predicts more realistically that $\bar{Z}$ will be proportional to total nutrient content T, and for fixed T will be a saturating (hyperbolic) function of the specific algal growth rate a_t. It also predicts that the $\bar{P}$, $\bar{Z}$ equilbrium will always be stable; this stability would be lost under eutrophic conditions if it were further assumed that f_t is a monotonically decreasing function of P_t (the classic "paradox of enrichment" model; see McAllister et al. 1972). Finally, it is not critical for model 2 that the nutrient T be strictly conserved; the same effect would be obtained if nutrient losses from the euphotic zone (outflow, sinking) are roughly balanced by inputs (inflow, advection–diffusion from hypolimnion). The positive effect of zooplankton nutrient excretion on phytoplankton production is implicitly recognized, since any net loss from the bound pool $n_Z Z$ will automatically cause the growth rate a_t ($T_t - n_P - n_Z Z$) to increase.

Models 1 and 2 fail to predict the widely observed pattern that total summer phytoplankton biomass is positively correlated with early spring nutrient content or loading (Dillon and Rigler 1974; Prepas and Trew 1983; Stockner and Shortreed 1985; McQueen et al. 1986). The general structures of eq. (1) and (2) can only make such predictions if F_t and/or M_t depend in some way on Z. One possibility is that F_t is a decreasing function of Z, since increasing Z may favor less vulnerable (larger cells, etc.) algal forms. The average filtering rate is in fact a weighted average: $F_t = \Sigma_i f_i B_i / P_t$ across phytoplankton types i with type-specific filtering rates F_i and biomass contributions B_i to the total P_t. If the biomasses B_i associated with high f_i do decline as Z increases, we might expect to see the weighted average F_t decrease according to some relationship; one possible algebraic form for this relationship is

$$(8)\quad F_t = \frac{f_0}{1 + f_h Z}$$

where f_0 is the maximum filtering rate (possibly time varying) and $1/f_h$ is the zooplankton biomass at which F_t is reduced to $F_0/2$. Substituting this relationship into eq. (2), and otherwise making the same assumptions as in model 2, we get the equilibrium conditions:

Model 3:

$$(9)\quad \bar{P}_t = \left(\frac{m_t}{f_0}\right) + \left(\frac{m_t f_h}{f_0}\right) \bar{Z}_t$$

$$(10)\quad \bar{P}_t = \frac{1}{a_t n_P}\left[a_t T - a_t n_Z \bar{Z}_t - \frac{f_0 \bar{Z}_t}{1 + f_h \bar{Z}_t}\right].$$

This model predicts a positive correlation between total algal biomass $\bar{P}_t$ and zooplankton biomass $\bar{Z}_t$, and it predicts that both $\bar{P}_t$ and $\bar{Z}_t$ will be positively correlated with total nutrient loading T. The relationship is algebraically complex and need not be presented here; it should be approximately linear if f_h is large (so that phytoplankton composition effects are seen even at low Z values). Empirical regression analyses have found the $\bar{P} - \bar{Z}$ (or Chl $a - \bar{Z}$) relationship to be weak (small value of f_1) compared with the $T - \bar{Z}$ and $T - \bar{P}$ relationships (reviews in Hanson and Peters 1984; McQueen et al. 1986). It is important to note that model 3 makes predictions about total algal biomass, while models 1 and 2 refer only to grazable algae without admitting variations in grazability within the grazable biomass pool. One way to derive eq. (8) is to assume that the total P_t consists of two biomasses, say all single cell forms B_1 and all colonial forms B_2 where B_1 has filtering rate f_0 and B_2 has zero filtering rate and is positively correlated with Z (this correlation is expected if nutrient availability or regeneration rates increase with zooplankton abundance while the biomass B_1 is held down by grazing and so cannot take up all of this nutrient).

The arguments about algal composition that lead to eq. (8)–(10) could be applied to the other terms in eq. (1) and (2) to give a variety of more complex models of $\bar{P}_t$ and $\bar{Z}_t$. However, such complications would not lead to qualitative predictions much different from model 3, unless nonmonotonic relationships were assumed for the specific rate components (e.g. Holling 1965 type III feeding response for zooplankton). As we shall see, such complications are not necessary to explain the observed behavior of the four lakes studied here.

Likely magnitudes and temporal patterns of variation in α_t, F_t, and M_t can be established from the literature and from experiments on our lakes. Values of α_t are expected to vary from 0 to around 1.0/d and to be roughly proportional to daily insolation (photoperiod × light intensity) and free nutrient concentration. Enclosure experiments by Krause (1984) in Placid Lake indicate that daily $\alpha_t = 0.5$ after phytoplankton biomass had been reduced and the water column fertilized by short periods (48 h) of high zooplankton grazing. Based on recent surveys (Peters and Downing 1984; Chow-Fraser and Knoechel 1985) and grazing experiments with various zooplankton species from all four lakes (Buckingham 1978; Krause 1984), we expect F_t to be nearly temperature independent and to be around 1.0–5.0 mL·μg zooplankton biomass^{-1}·d^{-1}. Some field studies of metabolic rates (Duval and Geen 1976; Andrew 1985) also suggest that M_t may be nearly temperature independent under natural (acclimated) conditions and should be in the range 0.1–0.4 μg·μg zooplankton biomass^{-1}·d^{-1}.

Figure 2 shows simulations of how well the equilibrium predictions of model 2 are likely to be tracked (by the differential equations (1) and (2) with model 2 assumptions) for two values of a_t and fixed values of $f_t = 3.0$ and $m_t = 0.3$. Here for convenience, we drove the simulations with measured time series of total insolation in the study area (see below), assumed a_t proportional to insolation, and took $T = n_P = n_Z = 1.0$ (i.e. biomasses measured in nutrient units). Under these assumptions, the equilibrium P_t is constant (eq. (6) with no seasonal changes in m_t, f_t) and the equilibrium Z_t is nearly proportional to insolation (see Fig. 3). It is clear from the simulations that the equilibrium values $\bar{P}_t$ and $\bar{Z}_t$ should be tracked quite closely if α_t, F_t, and M_t are in the ranges expected. This tracking ability is lost if a_t is much smaller (0.01–0.1/d) than expected. The simulations show some predator–prey oscillation around the equilibrium patterns. Such oscillations are exaggerated by

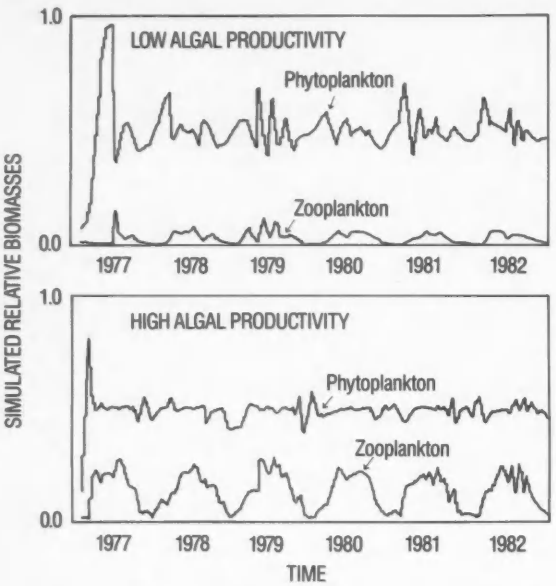

FIG. 2. Simulations of grazable phytoplankton and total zooplankton biomasses for the period 1976–82, using the simple model 2 (see text) with algal growth a_t proportional to solar insolation (from Fig. 3) and constant (temperature independent) zooplankton filtering (f = 3.0 mL/μg) and metabolic (m = 0.3 $\mu g \cdot \mu g^{-1} \cdot d^{-1}$) rates. Simulated values are "sampled" on the same dates as for the field data (Fig. 4). For the low-productivity scenario, a_t was chosen to give a maximum algal biomass growth rate (under longest photoperiod, total nutrients T = 1) of round 0.2/d; for the high-productivity scenario, this maximum would be around 0.8/d.

assuming a decrease in F_t with increasing P or by increasing the total nutrient content T, and are reduced by including the model 3 assumptions about decreasing filtering rate with increasing Z. The simulated zooplankton biomass oscillates much more than the phytoplankton biomass, especially for the low a_t case. Murdoch and McCauley (1985) noted this pattern in their survey of *Daphnia*–algae dynamics, but apparently did not recognize that it would be predicted by simple models not involving *Daphnia* size/age structure or algal composition changes.

Based on the equilibrium equations and the simulations, we make five general predictions concerning oligotrophic lakes:

(1) The biomass of grazable phytoplankton should show no spring bloom or other seasonal cycles, and should on average be equal to the zooplankton metabolic rate m_t divided by the average zooplankton filtering rate f_t.

(2) The biomass of grazing zooplankton should be proportional to the algal biomass growth rate a_t (i.e. should be proportional to light and/or temperature and nutrient loading, assuming that a_t is proportional to these factors).

(3) Zooplankton densities should decrease with increasing water depth (due to decreasing a_t at lower lights levels), but grazable algal density should be independent of depth.

(4) Fertilization should not change prediction (1) except to introduce short-term oscillations and favor biomass development of ungrazable algal forms; however, the zooplankton biomass should respond strongly as in prediction (2).

(5) Changes in the predation pattern on zooplankton (e.g. by fish introductions) should cause increases in phytoplankton biomass only in so far as the zooplankton community favored by predation has a different ratio m_t/f_t than the original community.

Note that we have not predicted that total primary production rates or total phytoplankton biomass (or indices such as Chl *a* concentration) should be independent of season or lake fertility. The basic prediction is simply that changes in productivity should be "pumped" through to zooplankton biomass, without the "pipeline diameter" (grazable phytoplankton biomass) changing appreciably. Nor are we claiming that the primary production rate ($\alpha_t P$) should be strongly influenced by grazing, except in so far as this rate is limited by the biomass of grazable phytoplankton. Finally, we do not claim that the predictions will extend to eutrophic lakes, where earlier modelling (Walters et al. 1980) indicates that biomasses should be dynamically more unstable and may be strongly influenced by high concentrations of detrital material (which influence zooplankton filtering rates and provide a nutritional pathway to the zooplankton from primary production sources other than grazable phytoplankton).

The predictions could fail in two ways that would lead us to reject the simple models. First, it could be that the P–Z interaction is dynamically unstable, with blooms and subsequent overgrazing in an oscillatory pattern such that equilibrium is never approached; from results in May (1973, p. 42), we would expect the period of such oscillations to be about $2\pi (a_t m_t)^{-1/2}$ d, i.e. 20–40 d based on available data on a_t and m_t. Second, it could be that zooplankton biomass is limited by some factor besides food supply, such as predation; in that case, there should be no obvious seasonal cycle (no summer peak) in zooplankton biomass but there should be a seasonal cycle in grazable algal biomass, with biomass peaking at times (and depths) that are favorable for primary production.

Field Methods

The four lakes (Fig. 1) were sampled about every 2 wk from mid-April to early December 1973–83, although the sampling season was occasionally lengthened (1976, 1979–80) or shortened by access difficulties or ice cover. Zooplankton and temperature were sampled throughout the study, while phytoplankton sampling began in 1974. However, we have discarded the 1974–76 phytoplankton data; the samples over that period were collected with Van Dorn bottles and filtered for counting; later, pump sampling and settling chamber counts indicated that the filtration method had led to gross underestimates of cell counts and biomass.

Zooplankton were sampled with a metered Clarke–Bumpus net (158 μm) towed diagonally through several depth strata (0–2, 2–4, 4–7, 7–10 m, and 10 m to near bottom, ending with 4–6 m for Placid) along midlake transects 100–200 m in length so that each tow would cover one quarter to one half of the longest axis of each lake; tow speeds were around 1.5 m/s, and the average sample volume was around 0.5 m^3. Early studies (Fedorenko 1973) had indicated that the repeatability of such long tows was about ±5%, so replicate tows were not taken for each depth–lake–date stratum. Subsamples for counting were taken with a plankton splitter, so as to give at least 200 individuals (when possible) for the dominant species. Five to ten body length measurements were taken for the dominant groups (juvenile and adult *Daphnia rosea*, juvenile and adult *Holopedium gibberum*, juvenile and adult *Diaptomus* spp.). Length–dry weight relationships were estimated for

these groups from fresh samples taken in three summers and were used to estimate biomasses in conjunction with the counts and length measurements. Our interest was originally in species composition and body size responses to the fish introductions. In hindsight it would have been better to directly weigh zooplankton samples to estimate biomass, since the small sample sizes for body lengths have introduced a substantial random error into the biomass estimates (standard deviation 8–12% of biomass estimates).

Beginning in 1977, phytoplankton were sampled with small water pumps (Coleman camper and bilge) through a 5-mm hose attached to the Clarke–Bumpus cable and weight. This system allowed us to take long diagonal tows (50–100 m) along the same transects as the zooplankton samples, across 2-m depth strata from the surface to 12 m (6 m in Placid Lake). Generally, one tow was taken for each depth–lake–date stratum, after preliminary replicate samples indicated a good repeatability (±10%) between tows. The samples were preserved in Lugol's solution and counted on inverted microscopes using the Utermohl technique. Cells were counted by size groups (<2 μm, 2–5 μm, ..., colonies), with enough microscope fields to insure that at least 200 cells were counted for the more abundant 2–5 μm size group. Taxonomic composition and cell shape information was regularly recorded, and this information was used to estimate an average cell volume for each group. The estimated dry weight biomass for each sample was assumed to be 0.3 times the estimated total cell volume (Peters and Downing 1984). This procedure was used for biomass determination (instead of direct sample weighing) because the lakes have relatively high concentrations (0.4–0.6 mg/L dry wt.) of suspended detrital material, mostly in the 0.5- to 2-μm size range.

Three physical time series were gathered as indices of seasonal changes in productivity. Water temperature was measured at 1-m depth intervals, 0–12 m, at midlake stations on all sampling dates. Daily sunlight hours and precipitation (an index of nutrient inflow rates) data are available from a weather station 5–7 km from the lakes at the southern edge of the University of British Columbia Research Forest (Fig. 1). The sunlight data were converted to daily irradiance estimates using an empirical relationship based on 2 yr of pyranometer measurements by M. Feller (Forestry, University of British Columbia, Vancouver, B.C., pers. comm.).

Enclosure experiments were carried out with various sizes of large plastic columns suspended from wooden frames near the lake shores. The columns had mouth sizes ranging from 0.25 to 1.7 m^2 and hung from the surface to depths ranging from 3 to 10 m. The columns were seeded with spatially mixed plankton assemblages gathered by towing a large 76-μm-mesh plankton net (1-m^2 mouth) or water pump (3-cm-diameter hose) in the vicinity of the columns while raising or lowering the device to obtain a vertically mixed sample. The columns were sampled for phytoplankton and zooplankton at 1- to 7-d intervals with a bilge pump, usually at several depth strata, so as to obtain 10–100 L/sample. Samples were processed with essentially the same procedures as described above.

Zooplankton filtering rates were estimated over a range of seston concentrations for 53 species–size–lake–date cases in 1977 (Buckingham 1978) using the ^{32}P-labelled yeast procedure of Burns and Rigler (1967), Burns (1969), Haney (1971), and Crowley (1973) and using cell count changes associated with high zooplankton concentrations in field enclosures in 1981 (Krause 1984). For the labelled yeast procedure, animals were transported from the field (2 h of travel) to our laboratory and then held in 100- to 500-mL beakers and 50-mL volumetric pipettes for 2 h to 5 d at various seston concentrations created by filtering lake water with a 100-cm-diameter 0.45-μm Millipore filter (well washed). Then, 600–6000 cells/mL labelled yeast were added to the containers for a 5- to 10-min grazing period. Effects of variables such as container size, holding time, and grazing period were determined from a series of experiments detailed in Buckingham (1978). The field enclosure procedure of Krause (1984) involved adding 5–10 times normal zooplankton densities of selected species to 150-L enclosures and measuring phytoplankton concentrations (cell counts by same procedure and size categories as for field monitoring) every 4–6 h for 48–72 h. Such experiments were conducted four times (10 bags/time) from June to September 1981 in Placid Lake only. Krause's experiments showed some differences in apparent grazing rates among algal size groups, as expected from other studies (Porter 1973; Frost 1977; Gliwicz and Siedlar 1980; Lehman and Sandgren 1985); only average rates across all unicellular size classes were used in the analyses presented here.

Metabolic rates of the zooplankton community were estimated in Gwendoline Lake on four dates in 1985 by 24-h in situ incubations of 300-mL BOD bottles with various zooplankton densities (Duncan et al. 1970; Cornett and Rigler 1986). On each date (Table 3), we suspended nine BOD bottles at each of three depths (surface, thermocline, below thermocline) with animals collected from (and presumably acclimated to) those depths using a slowly towed (0.5 m/s) Clarke–Bumpus or Wisconsin net (No. 10 mesh). The bottles for each depth were arranged in three groups, with one light bottle and two dark bottles in each group. The first group had natural zooplankton densities (0.02–0.1 mg/L; never enough to cause O_2 depletion in 24 h), the second had 0.5–1.0 mg/L zooplankton biomass, and the third had 1–2 mg/L zooplankton. Initial and final O_2 values were measuresd for each bottle using a YSI model 57 O_2 meter with a YSI model 5720A probe (with a battery-driven stirrer; control checks on bottles without initial measurements showed that the initial stirring did not affect later respiration rates). The higher zooplankton densities were selected so as to give expected O_2 depletions of around 0.5–1.5 mg O_2/L over the 24-h period. Two zooplankton densities were used to test for possible effects of density on respiration rates (reduced respiration rates were noted by Duval (1973) for Eunice Lake zooplankton crowded to above 3 mg/L; see also review in Andrew 1985); no such effects were observed, and we estimated respiration rates as the slopes of the regressions between O_2 consumption per 24-h versus zooplankton biomass. Variation in initial measurements among bottles indicated that the meter had good reproducibility (±0.02–0.05 mg/L) within a single measurement session; meter drift between sessions (over 24 h) might have created larger errors (±0.2 mg/L), but we controlled for this drift by measuring respiration as the slope of the graph of O_2 change versus zooplankton density (drift should affect the intercept, but not the slope, of this graph).

Results

The four lakes had similar phytoplankton and zooplankton communities, and only a few changes in species composition occurred in response to the various disturbance experiments. The phytoplankton communities were dominated (>50% of biomass) at most times by unicellular algae in the 6- to 10-μm

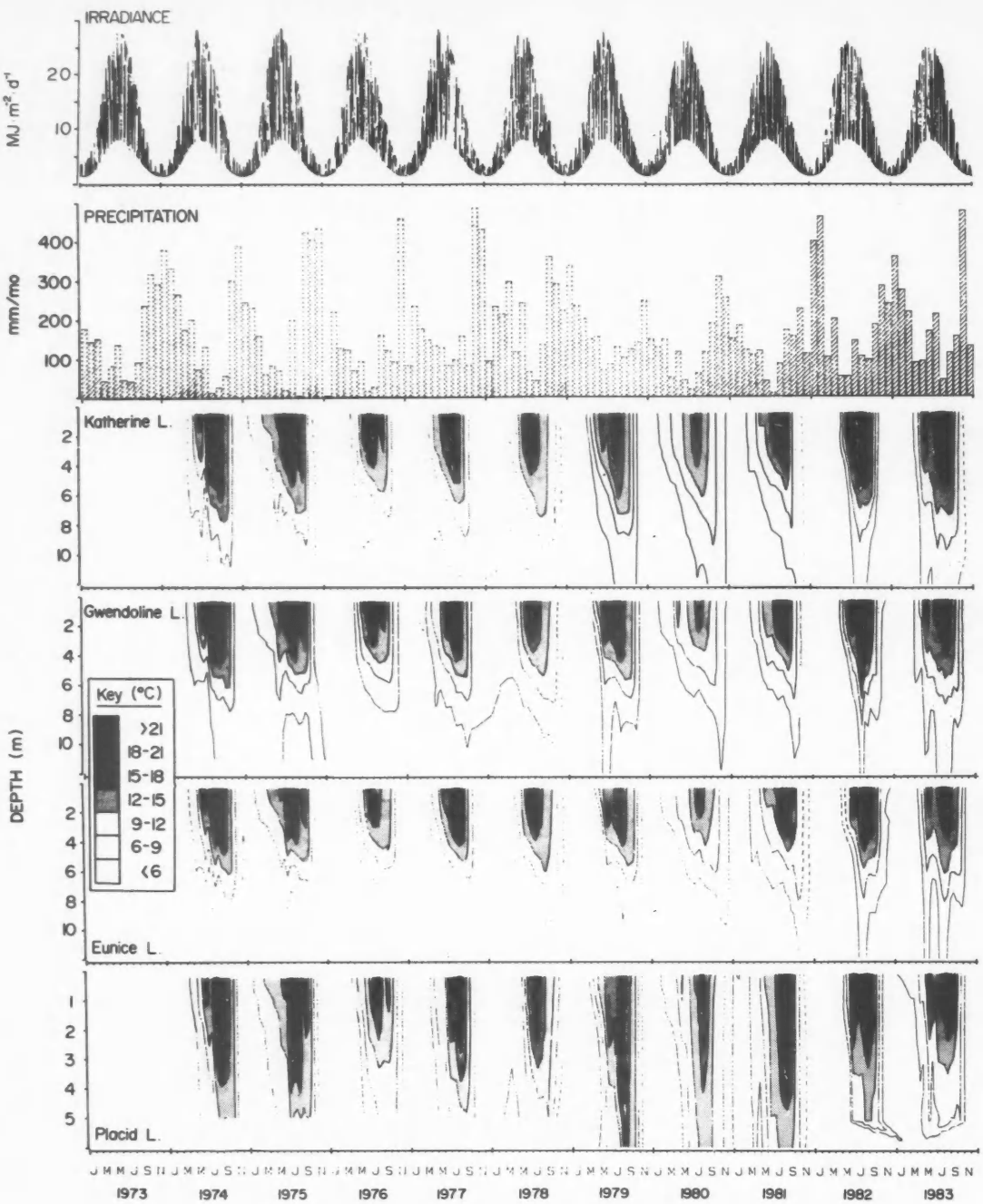

FIG. 3. Solar insolation, rainfall, and water temperature regimes in the study lakes.

size range, with the main types in this range being *Oocystis* and *Ochromonas*. Cells larger than 20 μm and colonial forms generally made up around 10–30% of the biomass, with the most common forms being *Gloeocystis* and *Merismopedia*. Rotifers were apparently rare in unfertilized situations (Neill 1984), and the zooplankton biomass was dominated in most years by *Daphnia rosea*, *Holopedium gibberum*, *Diaphanosoma brachyurum*, *Diaptomus kenai*, and *Diaptomus leptopus* (or *D. oregonensis* in Placid). *Diacyclops thomasi* was usually present as a small percentage of the biomass, and it increased dra-

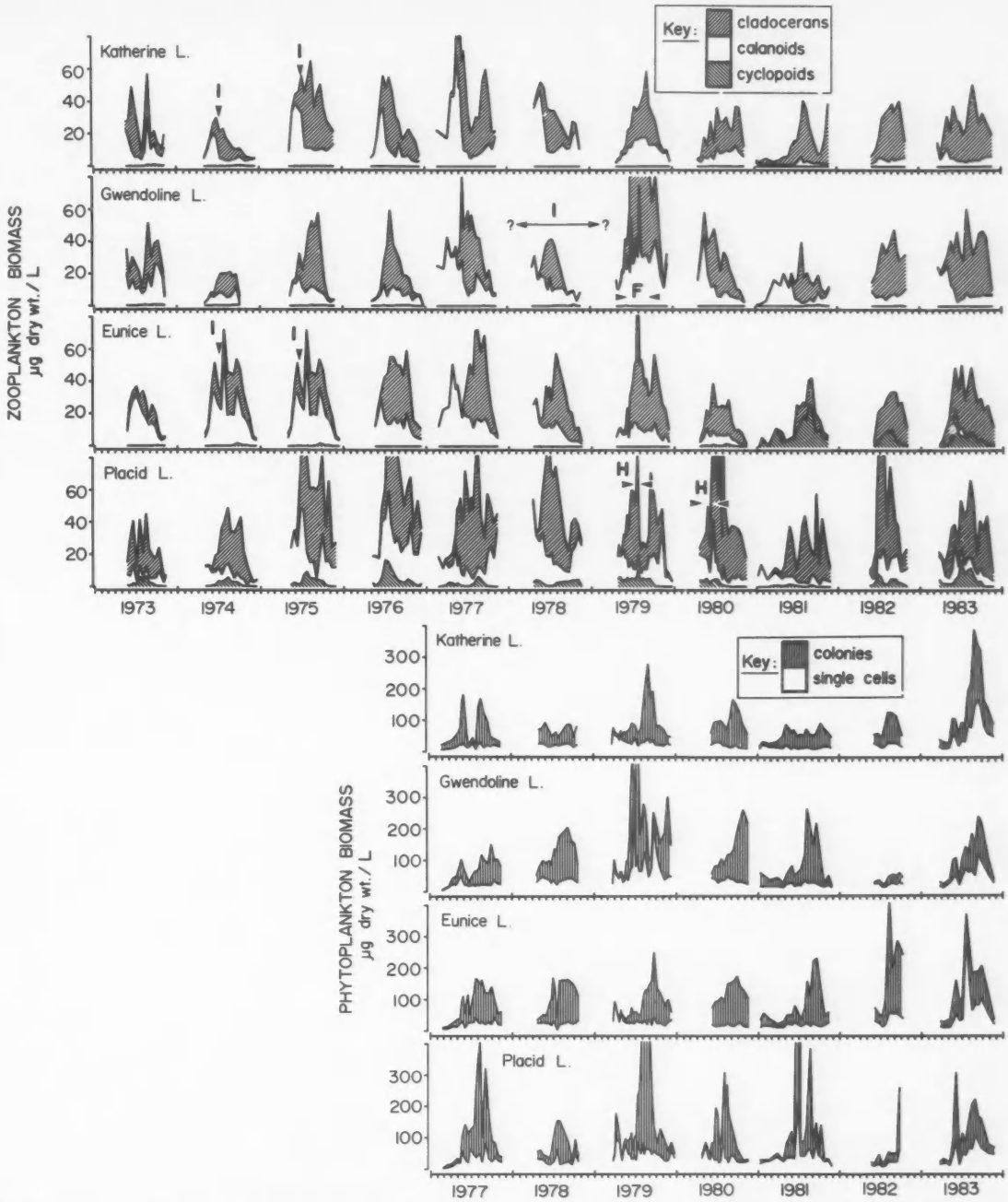

FIG. 4. Temporal patterns of phytoplankton and zooplankton biomass, as averaged concentrations over the sampled water columns (usually 0–20 m for zooplankton and 0–12 m for phytoplankton). Note that the Gwendoline Lake data for 1979 (fertilization year) grossly exceed the graph scales here (see Fig. 5). Fish introductions marked by I, fertilization (Gwendoline) period by F, and experimental zooplankton harvesting (Placid) by H.

matically in 1980 in Eunice Lake so as to make up 90% of the spring and early summer biomass for 2 yr. The main predators on zooplankton in Gwendoline, Eunice, and Katherine lakes prior to fish introductions were *Chaoborus trivittatus* and *C. americanus* (Fedorenko and Swift 1972; Fedorenko 1975; Swift and Fedorenko 1975; Northcote et al. 1978; Neill 1981b); these species were quickly (one to two seasons) eliminated by the fish after each introduction (Northcote et al. 1978). In

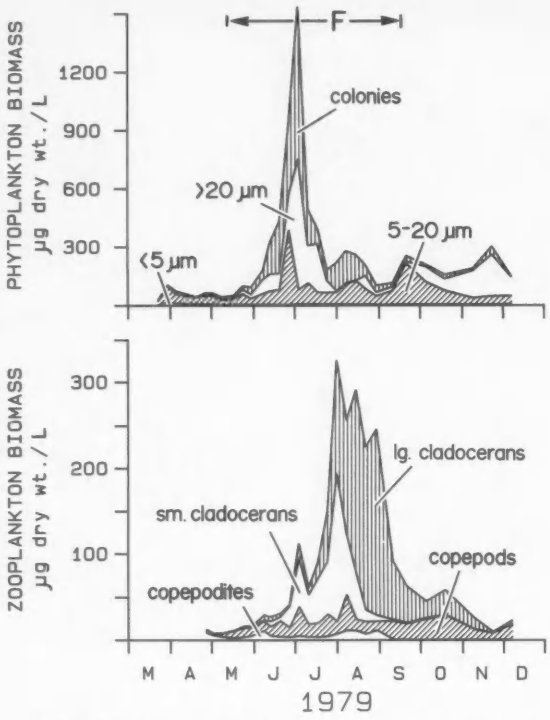

FIG. 5. Phytoplankton and zooplankton responses to fertilization in Gwendoline Lake, 1979. Fertilizer was applied weekly over the period May 15 – September 1. Compare with Fig. 4.

Placid Lake, *Chaoborus flavicans*, *Polyphemus pediculus*, and *D. thomasi* were abundant zooplankton predators.

Seasonal Biomass Patterns

There was substantial interannual variation in solar insolation and rainfall on the study area and in water temperature regimes (Fig. 3). Unusually cool, wet summers occurred in 1975 and 1981, and unusually dry, cold winters occurred in 1976–77 and 1981–82. A prediction from the theory presented earlier is that such variations should influence zooplankton biomass patterns (through impacts on rates of primary production), but should have little effect on grazable phytoplankton biomasses.

As predicted by models 1 and 2, there were clear seasonal cycles in depth-averaged zooplankton biomass in all lakes and years, with usually a single midsummer biomass peak, but no obvious seasonal cycles in biomass of unicellular phytoplankton except in 1983 (Fig. 4). Changes in biomass of unicells were small in comparison with colonial forms and were correlated with changes in zooplankton biomass. The unicellular forms are mainly <30 µm in diameter and are presumably mostly grazable. Colonial forms (mainly >60 µm in diameter colonies, shaded areas in Fig. 4) showed a seasonal rhythm correlated with zooplankton biomass, as predicted by model 3. Simple nonequilibrium models would predict spring phytoplankton peaks followed later by zooplankton peaks. Only in 1983 was a clear seasonal cycle in unicellular phytoplankton evident in unfertilized lakes; in that year, biomass generally increased in all four lakes until late August or early September and then declined. Nonequilibrium behavior was evident in Gwendoline Lake in 1979, where the dramatic response to fertilization involved a phytoplankton bloom followed by a zooplankton peak and a persistent increase in the biomass of large, presumably less grazable algal forms (Fig. 5). However, notice in Fig. 5 that the nanophytoplankton biomass quickly returned to the "normal" level of around 0.1 µg/mL dry mass and remained quite stable in spite of major changes in zooplankton and large algal forms.

Biomass depth distributions also behaved as predicted by the models (Fig. 6). Unicellular phytoplankton biomass showed no clear depth pattern; occasional peaks occurred in deeper water during summer due to dense layers of large algal forms (particularly *Gloeocystis*) apparently associated with the thermocline. On the other hand, zooplankton biomasses were concentrated near the surface in spring and fall, and often showed a maximum at intermediate depths (4–7 m) in midsummer. It appears that zooplankton biomasses followed a typical depth pattern for primary production rates in temperate lakes, but it would be premature to claim that all depth strata remained near dynamic equilibrium due to the growth-loss mechanisms of eq. (1) and (2). We have no information on vertical mixing rates of phytoplankton, and a few of the zooplankton species have exhibited diurnal migrations (Fedorenko 1973) and diurnal changes in filtering rates (Duval and Geen 1976; Haney 1985) that might cause a short-term averaging of the depth distribution of filtering impacts.

Plots of the relationship between grazable phytoplankton biomass and insolation or water temperature should theoretically show no pattern; it is obvious from Fig. 3 and 4 that this is the case for most lake–year combinations, since there were no seasonal patterns in unicellular algal biomass. For total phytoplankton there were significant and positive regressions of biomass on insolation and surface water temperature (Table 2). On the other hand, there should be a good correlation between zooplankton biomass and insolation, and perhaps also with temperature. However, the zooplankton correlations (Table 2) are not as strong as might be expected from Fig. 3 and 4. Various dips and peaks lasting for more than one sampling period (and thus not likely due to random sampling errors in the biomass estimation) cannot be explained by monotonic variation in Z_t with measured changes in insolation or temperature (Fig. 4, note: Katherine Lake, 1977 and 1981; Gwendoline Lake, 1973; Eunice Lake, 1977, 1979, and 1981).

Impacts of Fish Predation and Zooplankton Harvesting

Placid Lake had an established trout population, and the introduction of several hundred adults to Katherine (char) and Eunice (cutthroat trout) lakes in 1974–75 (see Hume and Northcote 1985 for details) led to flourishing, self-reproducing populations by the late 1970's. Following failure of a barrier on the stream connecting the lakes, juvenile trout from Eunice Lake began invading Gwendoline Lake by 1978. Shortly after introductions, the trout were observed to feed mainly on *Chaoborus* spp. and *Daphnia rosea* along with benthic insect fauna, although some *Diaptomus kenai* and *Holopedium gibberum* were also eaten (Hume and Northcote 1985). In later years in these lakes, and for all years in Placid Lake, casual sampling showed the fish feeding mainly on terrestrial and benthic insects.

Figures 4 and 6 indicate that there was little impact of the fish introductions and experimental zooplankton harvesting on the

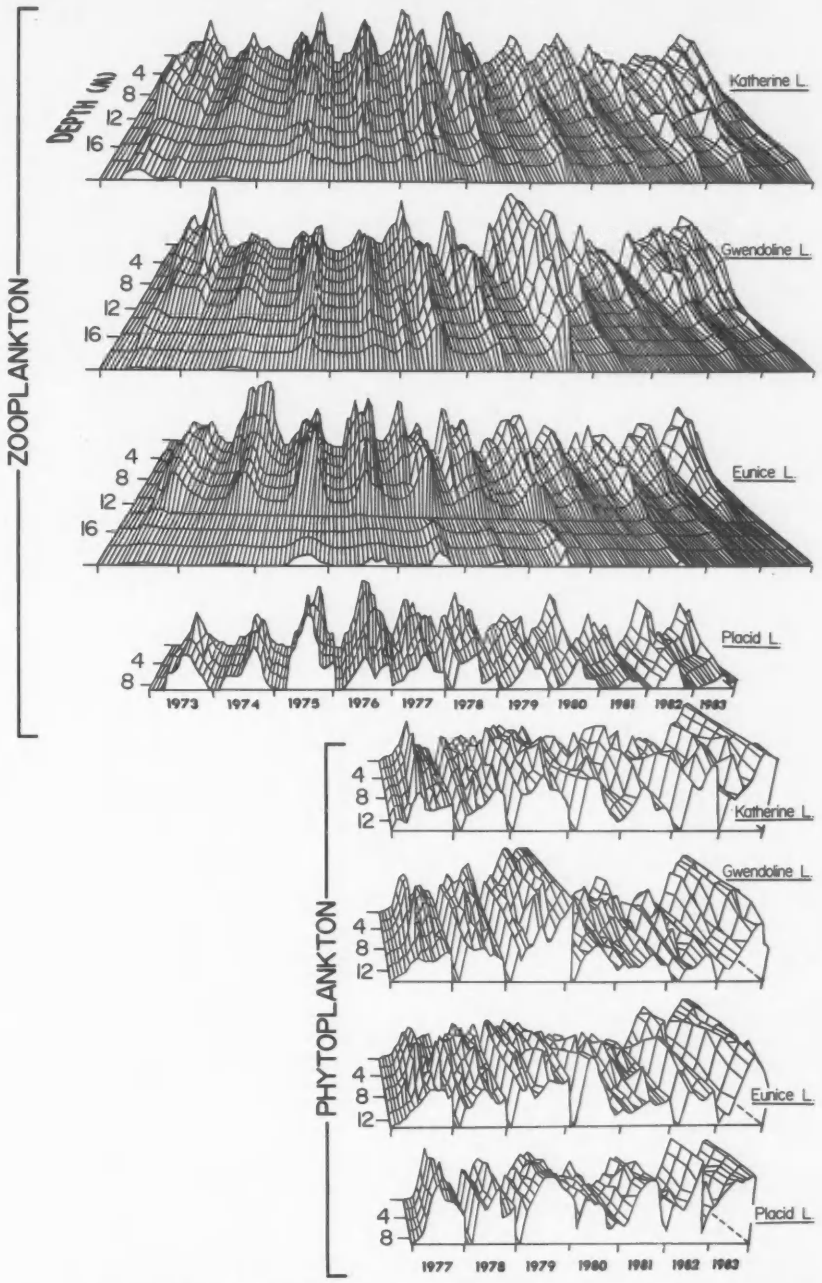

FIG. 6. Depth distributions of phytoplankton and zooplankton biomass in the study lakes. Compare with depth averages in Fig. 4.

seasonal pattern of total zooplankton biomass. Interannual variations in seasonal peak biomasses (high in 1977, low in 1978 and 1981, etc.) were apparently associated with factors that influenced the control lakes (Gwendoline and Placid) as much as the treated lakes. The main effect of the fish introductions, besides rapid removal of *Chaoborus trivittatus* and *C. americanus*, was a sharp decrease in the average body sizes of *Daphnia rosea* and *Diaptomus kenai*, a minor decrease in body size of *Holopedium gibberum* (Fig. 7, compare 1974–75 with later years; see also Northcote et al. 1978), and an increase in body size of *Bosmina longirostris*. These decreases were accompanied by increases in numerical abundance (of smaller indi-

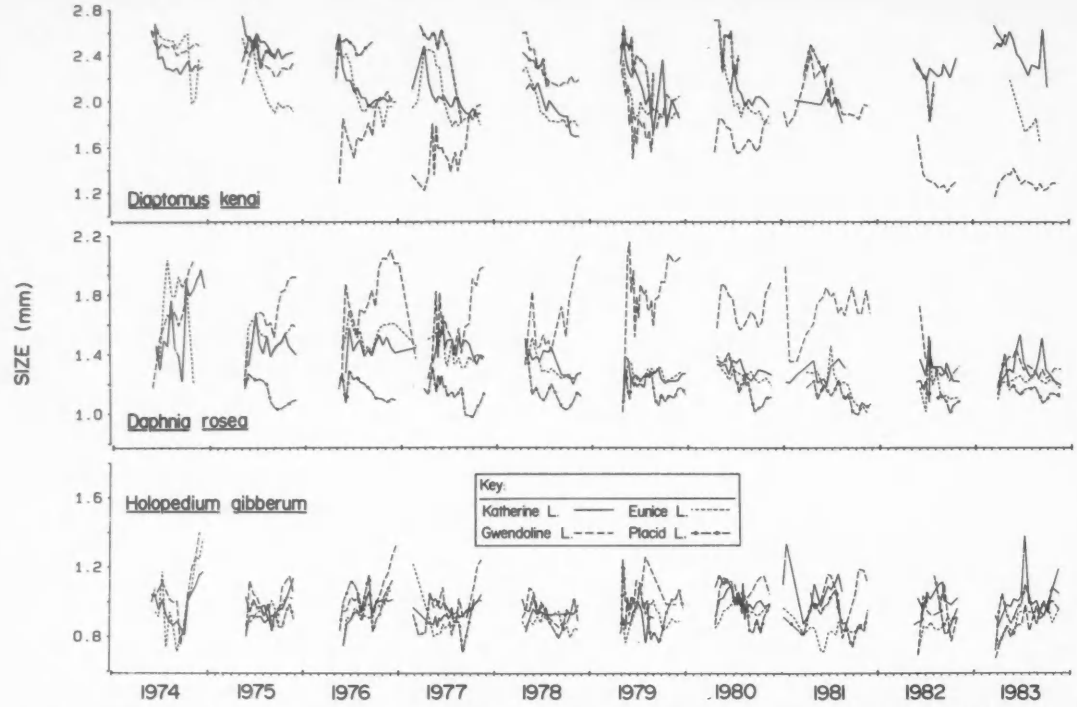

FIG. 7. Average body sizes for the dominant zooplankton species in the study lakes. Note that trout were introduced into Katherine and Eunice lakes in 1974–75 and invaded Gwendoline Lake in 1978–80; Placid lake had an established trout population over the whole study period.

TABLE 2. Slopes of regressions of depth-averaged total phytoplankton and zooplankton biomass on solar insolation and surface water temperature. Data from Fig. 3 and 4, using all sample dates. Significance of regression coefficients as indicated (ns = not significant, $*P < 0.05$, $**P < 0.01$). Gwendoline zooplankton slopes are similar to Katherine when 1979 fertilization data are omitted.

	Phytoplankton		Zooplankton	
Lake	Insolation	Temperature	Insolation	Temperature
Eunice	37 ns	99**	2.3**	1.8**
Katherine	41*	48**	4.1**	2.6**
Placid	169**	91**	6.7**	2.9**
Gwendoline	125*	84**	9.2**	7.4**

viduals) so that the biomass contributions of the major species were not consistently affected (Fig. 4). The increased abundances may have been due either to reduced intraspecific competition when large individuals were selectively removed by fish (Northcote et al. 1978; Hume and Northcote 1985) or to increased survival rates when predatory *Chaoborus* were eliminated; bag experiments by Neill (1981b) support the latter hypothesis. In terms of our theoretical predictions, the key question is whether the zooplankton filtering rates f_i or loss rates m_i changed significantly with the decrease in average body sizes. From experimental data, we expect that f_i (millilitres per microgram of zooplankton per day) increased (Buckingham 1978; Peters and Downing 1984; Haney 1985), but probably so did the metabolic component of m_i (because m_i is measured as a rate per unit biomass). The lack of difference in phytoplankton biomass between the fishless Gwendoline Lake (1977–78) and the fish-present situations (all other lakes–years for which phytoplankton was sampled) would be explained by the models as constancy in the ratio $P_t = m_t/f_t$.

The experimental zooplankton harvesting in Placid Lake in July–August 1979 appeared to result in biomass decrease and a bloom of the large ungrazable alga *Merismopedia* (Fig. 4). However, the May–July harvesting in 1980 produced no measurable response relative to other ("control") years. Neither of these results was as predicted by the simple models. We suspect that the towing procedure (net towed 20 m behind a small boat with 15-hp motor) caused considerable mixing of the water column and complicated changes in nutrient exchange patterns between surface and near-bottom (Z_m = 7 m).

Biomass Predictions from Filtering and Metabolic Rate Data

The filtering rates f_i estimated by Krause (1984) were generally in the range of 3–10 mL·μg zooplankton^{-1}·d^{-1}, while most of Buckingham's (1978) estimates were lower, in the range of 1–3 mL·μg zooplankton^{-1}·d^{-1}. From the studies of Duval and Geen (1976) in Eunice Lake, and our light and dark bottle experiments on zooplankton respiration (Table 3), we estimate that m_i must lie between 0.2 and 0.4 mg·mg^{-1}·d^{-1} and does not vary significantly with water temperature. Using these zooplankton functional data, the equilibrium theory predicts P_t to be in the range 0.02–0.2, with our best point prediction being 0.3/3 = 0.1 mg/L. This estimate is approximately double the average unicellular phytoplankton biomass (about 0.05 mg/L) observed in the field (Fig. 4) except during the transient response to fertilization in Gwendoline. It is possible that Krause's technique (cell count changes) was more

TABLE 3. Respiration rates of the zooplankton community in Gwendoline Lake during 1985, measured as biomass respired per day per unit biomass present on average during the day. Estimates obtained from slopes of regressions of total O_2 consumption over 24 h versus zooplankton biomass; numbers in parentheses are standard errors of the regression coefficients. In all cases, deepwater samples were incubated at 8–9 m at water temperatures of 5.0–6.0°C.

	Temperature (°C)		Respiration rate			
Date	Surface	Thermocline	Surface	Thermocline	Deep	Combined
June 5	13	8	0.45 (0.04)	0.22 (0.08)	0.09 (0.09)	0.37 (0.06)
June 26	16	9	0.41 (0.09)	0.44 (0.49)	0.10 (0.05)	0.26 (0.07)
July 18	22	14	0.51 (0.28)	−0.05 (0.10)	−0.05 (0.23)	0.37 (0.17)
August 7	20	12	0.52 (0.03)	−0.004 (0.06)	0.25 (0.06)	0.34 (0.03)

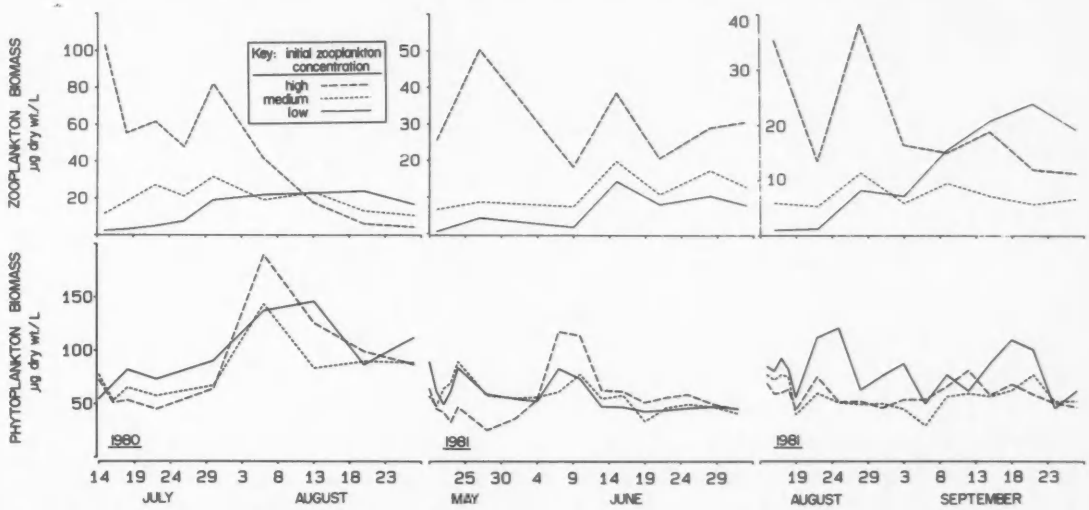

FIG. 8. Phytoplankton and zooplankton biomass changes in 0.25-m^2 × 3-m-deep enclosures, Placid Lake, 1981. The bags were treated by varying intial zooplankton populations as shown. (From Krause 1984.)

accurate than Buckingham's (labelled yeast), even though there are a variety of reasons to be more suspicious of it. Another possibility is that some of the larger algae (shaded area in Fig. 4) are in fact grazable; the transient response of all algal forms to fertilization in Gwendoline Lake (Fig. 5), with general declines associated with the zooplankton increase, supports this possibility.

Biomass Responses in Enclosures

A key assumption in the equilibrium theory is that P and Z can respond quickly to disturbances (or movement in P_t, Z_t) so as to reachieve equilibrium on time scales that are short compared with the time scales of variation in a_t, f_t, m_t, and the field sampling interval. We have limited data on response times from a set of enclosure experiments in Placid Lake, where initial zooplankton biomasses were varied and responses measured over a 30- to 40-d time scale (Fig. 8; details in Krause 1984). A confounding factor in these experiments was that variation in the initial zooplankton stocking rate probably led to substantial variation in the nutrient loadings of the bags; the total phosphorus level in Placid Lake averages around 10 µg/L (Werring 1986). By manipulating zooplankton biomasses over a range of 1–100 µg/L dry mass, we may have altered this total by up to 2 µg P/L, as well as influenced its availability over time. With this reservation, it appears from Fig. 8 that the phytoplankton biomass achieves a short-term equilibrium very quickly (in less than 10 d), while the zooplankton biomass may require 2–3 wk to reach a relatively steady level starting from 0.1–5 times this level. These response times are of the magnitude predicted by eq. (1) and (2) using realistic rate constants for a_t, F_t, and M_t (Fig. 2). However, longer-term (4–5 wk) responses were also seen in the phytoplankton in the 1980 experiment (Fig. 8).

In an effort to measure potential phytoplankton responses more precisely, Krause (1984) stocked a series of 300-L enclosures with very high zooplankton densities (1.5 mg/L) for 48 h to reduce the phytoplankton biomass (and enrich the enclosure due to zooplankton excretion) and then removed the zooplankton (or reduced zooplankton to lake levels) and monitored phytoplankton biomass every 4–12 h for 48 h (Fig. 9). These experiments show initial (12 h) intrinsic rates of increase for grazable phytoplankton of about 0.7/d. Diurnal phytoplankton biomass cycles seemed to occur in the enriched enclosures and in some 60- to 70-h enclosure experiments used to measure zooplankton filtering rates. These cycles had amplitudes of up to ±50% under enriched (by zooplankton excretion) conditions, suggesting that the net daily growth rate was in the range 0.2–0.4. In support of this lower estimate, the net daily growth rate of phytoplankton biomass shortly after fertil-

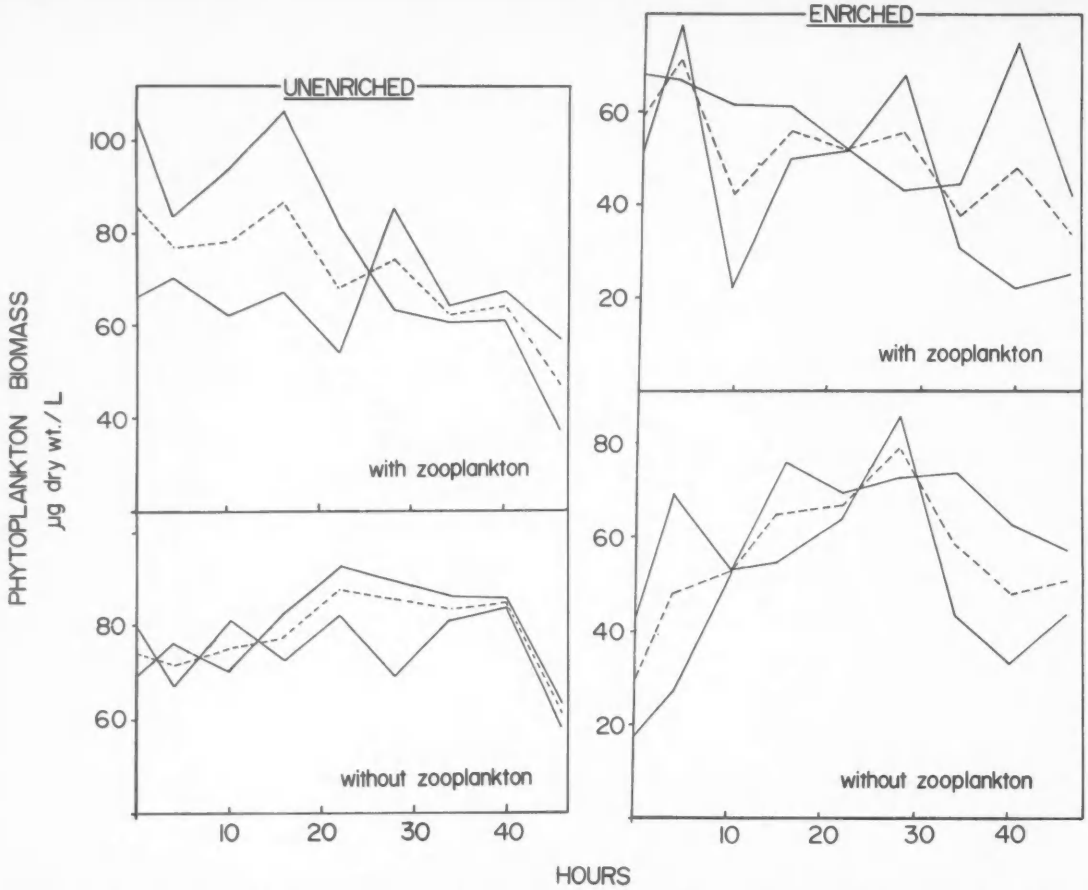

FIG. 9. Phytoplankton biomass changes in 300-L plastic enclosures, Placid Lake, late August 1981. The "enriched" bags were treated by adding very high zooplankton densities (1.5 mg/L) for 48 h prior to the sampling period shown. The "with zooplankton" enclosures were stocked at lake densities. Broken lines show means of the two enclosures for each treatment combination. (From Krause 1984.)

ization began in Gwendoline Lake in 1979 was about 0.1/d (Fig. 5); during this growth period the loss due to grazing likely averaged about 10%/d.

Discussion

Table 4 reviews general predictions from the three simple models in relation to observed qualitative patterns. Model 1 fails on most counts, since it incorporates no mechanism to prevent short-term cycles in biomasses. Model 2 explains most observed patterns, except seasonality in total phytoplankton biomass and lack of response to predation on zooplankton. Model 3 "improves" on model 2 in predicting seasonality in total phytoplankton biomass, but incorrectly predicts that phytoplankton biomass should decrease at greater depths.

Peak zooplankton biomasses in the four lakes during summer were generally in the range 50–100 µg/L. If filtering rates were around 3 $mL \cdot \mu g^{-1} \cdot d^{-1}$ at these times, the grazers removed only 15–30% of the phytoplankton biomass per day. This estimate seems low compared with peak exploitation rates reported in the literature (Haney 1973), although it is higher than the overall rate inferred for nearby lakes (San Juan Island, Washington) with high zooplankton biomasses by Lehman and Sandgren (1985). However, the key point is not its absolute magnitude but rather whether it is high enough to balance the phytoplankton biomass growth rate. Such a midsummer balance seems likely in view of the 20–40% estimate for net daily growth rate from enclosure experiments and from the Gwendoline Lake fertilizer response. However, grazing loss rates in spring and fall must be much lower, on the order of 5–10%/d of the phytoplankton biomass; it is difficult to believe that the phytoplankton growth rate is so low at these times.

There are at least two possible explanations for the observed seasonal patterns of plankton biomass. First, it may simply be that these oligotrophic lakes have very slow biomass turnover rates, with severe nutrient limitation preventing phytoplankton blooms and permitting only modest development of zooplankton stocks. This model is implicit in much of the literature comparing oligotrophic and eutrophic systems, and it is consistent with our observation of blooms following fertilization of Gwendoline Lake. However, it is not consistent with our estimates of phytoplankton turnover rates due to grazing, estimates of zooplankton metabolism, and the evidence from enclosure

TABLE 4. Summary of predictions from models 1–3 compared with observed plankton patterns.

Response measure	Model predictions			Observed pattern
	Model 1	Model 2	Model 3	
Grazable phytoplankton biomass	Cyclic[a]	Constant[b]	Seasonal	Constant
Total phytoplankton biomass	Cyclic	Constant	Seasonal	Seasonal
Phytoplankton response to fertilization	Cyclic	Cyclic/constant	Increase	Cyclic/constant
Zooplankton biomass	Cyclic	Seasonal	Seasonal	Seasonal
Zooplankton response to fertilization	Cyclic	Increase	Increase	Increase
Phytoplankton depth distribution	Cyclic	Constant	Increasing	Constant
Zooplankton depth distribution	Cyclic	Decreasing	Decreasing	Decreasing
Phytoplankton response to fish predation	Increase/ cyclic	Increase	Increase	None
Phytoplankton response to zooplankton harvesting	Violent increase	Increase[c]	Increase[c]	Mixed

[a]Predator–prey cycles with 20- to 40-d period.
[b]No spiky blooms or seasonal peak in midsummer.
[c]Increase should be slight (10–20%), since limited by removal of nutrients with the zooplankton.

experiments of quite rapid biomass changes. These data support a second explanation, namely that biomass turnover rates are quite rapid (at least 20%/d for zooplankton, even higher for phytoplankton), and there exist strong mechanisms (as proposed in models 2 and 3) to keep biomasses near equilibrium. Rapid turnover rates, and perhaps also tight biomass regulation, have been proposed for the smaller phytoplankton components of aquatic systems by other researchers (Goldman and Gilbert 1983; Welschmeyer and Lorenzen 1985; Lehman 1987): diurnal algal biomass changes have been observed even in Arctic lakes (Kalff and Welch 1974).

Models 2 and 3 propose two mechanisms by which the phytoplankton–zooplankton interaction may be stabilized so as to prevent strong biomass oscillations (blooms). First, model 2 hypothesizes that strong nutrient limitation of phytoplankton growth rates (through the term $T - n_P P - n_Z Z$) acts in concert with seasonal variations in growth rate (a_t) due to light/temperature. Such feedback on prey growth generally has a strong stabilizing effect in predator–prey models (Rosensweig and MacArthur 1963). Total phosphorus levels and enclosure experiments involving zooplankton removals both indicate that the "carrying capacity" level for phytoplankton biomass in the absence of grazing would not be much higher than observed under normal conditions. The additional limiting effect of grazing (to $P_t = m_t/f_t$) became evident after fertilization in Gwendoline Lake, where we observed only a short transient departure from normal biomass levels for small celled phytoplankton (Fig. 5, June–July). Second, model 3 proposes decreases in grazing efficiency as total nutrient loading is increased (F_t a decreasing function of zooplankton biomass), through selection favoring (or competitive advantage to) less grazable algal forms. In terms of predator–prey theory, this mechanism causes the zooplankton isocline to have a positive slope (i.e. not vertical), another condition that favors stability of the predator–prey equilibrium. Along with shifts in algal size composition, model 3 predicts an asymptotic relationship between nutrient loading and zooplankton biomass; enclosure experiments by Neill (1984, fig. 4) in Gwendoline Lake support this zooplankton prediction, although he did not see large changes in phytoplankton composition.

A surprising feature of the field data is the apparent absence of biomass responses to major changes in zooplankton size and species composition, including even the years in Eunice Lake when there was a near monoculture of *Diacyclops thomasi*. In fact, models 1 and 2 predict just this result. Phytoplankton biomass should be proportional to the ratio of zooplankton total loss to filtering rates per biomass, and these rates are in turn expected to be decreasing functions of the average zooplankton body size. It appears that the pattern of decrease in both rates was similar enough to make the ratio nearly constant. Likewise, zooplankton biomass should be proportional to the ratio of algal growth rate to zooplankton filtering rate and should be independent of the zooplankton loss rate, provided this rate permits persistence at all. It appears that the effective "filtering" rate f_t for *Diacyclops* nauplii and copepodites was not much different from the rate associated with the normal filter-feeding community.

The models suggest that the observed differences between years in zooplankton biomass patterns should be due to variations in the factors that affect primary production (a_t and total nutrient loading, T). Year-to-year differences in sunlight and temperature were not large enough to cause a_t variations that could explain the differences. There is a weak correlation between zooplankton biomass peaks and total precipitation as an index of nutrient loading from the watersheds (compare Fig. 3 and 4), but this correlation is not convincing. There was extensive logging in the Gwendoline and Katherine watersheds between 1968 and 1973. If these watersheds responded in a similar manner to others nearby in the Research Forest (Feller and Kimmins 1984; M. C. Feller, pers. comm.), then substantial increases in nitrate inputs should have occurred during the first 2–3 yr after logging and slash burning; this nutrient enrichment should then have declined in the mid-1970's to a nutrient minimum in the late 1970's, followed by normal nutrient loading thereafter. The annual differences in phytoplankton and zooplankton biomass for Gwendoline and Katherine lakes do not reflect this predicted pattern of nutrient loading (Fig. 4).

There was considerable year-to-year variation in the biomass contributions of different zooplankton species, with the relative abundances of *Daphnia rosea* and *Holopedium gibberum* being

particularly unpredictable. The filtering rate experiments of Buckingham (1978) suggest that *Diaptomus kenai* and *Holopedium* are cold-water forms, in the sense that maximum feeding rates at high food densities (but not filtering rates at normal food densities) decrease as temperature increases over the range of 8–20°C. *Daphnia rosea*, *Diaphanosoma brachyurum*, and *Diaptomus oregonensis* appear to be warmwater forms, with positive variation in maximum feeding rates over the same temperature range. Such differences in temperature adaptation, and perhaps other specializations related to factors such as algal food size and type, imply that the species composition may fluctuate considerably (and various species coexist), without there being any major departures from overall biomass equilibrium.

Our results support the general contention (Lynch and Shapiro 1981; Okansen et al. 1981; McQueen et al. 1986) that herbivores can regulate producer biomass in oligotrophic systems, but that producer biomass will increase under more productive conditions (midsummer growth of large algal forms, Gwendoline fertilization response). As suggested by McQueen et al. (1986), we also found that large *Daphnia* are not necessary to control phytoplankton abundance in our oligotrophic systems. In contrast with the predictions of Carpenter et al. (1985) and McQueen et al. (1986), we found little evidence of "top-down control" of grazing zooplankton biomass by fish or invertebrate predators; under changing predation regimes, we saw shifts in zooplankton body sizes that were apparently not large enough to cause changes in the ability of the zooplankton to control algal abundance. More dramatic impacts of fish predation (by juvenile sockeye salmon, *Oncorhynchus nerka*) on zooplankton have been noted in other oligotrophic lakes in British Columbia by Stockner (1987), and in those cases, it does appear that fertilization will lead to increased phytoplankton biomass when larger (>0.5 mm) zooplankton are rare (Stockner and Shortreed 1985).

The agreement between our equilibrium models and the field data lends credibility to the concept of using "loop analysis" (Lane and Levins 1977; Lane and Collins 1987) and related tools for making qualitative predictions about disturbed food webs. While we would not venture to claim that more detailed food web components (species or other taxonomic group) remain near equilibrium, that possibility deserves further study.

Our models and field results have at least two implications for environmental impact assessment and fishery management. First, we suggest that changes in zooplankton biomass levels should be a more sensitive indicator of changes in productivity of oligotrophic lakes than are algal biomass measures, such as chlorophyll *a* level, that have been commonly used. Second, we suggest that the seasonal responses of zooplankton biomass to deliberate fertilization can be predicted from simple models (2 and 3); such predictions are of value in fishery management insofar as total zooplankton biomass is a useful indicator of fish productivity.

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Reproductive Responses of Five White Sucker (*Catostomus commersoni*) Populations in Relation to Lake Acidity

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Trippel, E. A., and H. H. Harvey. 1987. Reproductive responses of five white sucker (*Catostomus commersoni*) populations in relation to lake acidity. Can. J. Fish. Aquat. Sci. 44: 1018–1023.

White sucker (*Catostomus commersoni*) in three acid lakes (pH 4.90, 5.56, and 5.58) frequently matured at older ages and larger sizes and had shorter reproductive life spans than white sucker in two circumneutral lakes (pH 6.30 and 6.35). Reproductive life span was positively correlated in females ($r = 0.97$) and males ($r = 0.85$) with lake pH. In the acid lakes, elevated mortality rates coincided with the onset of sexual maturity whereas in circumneutral lakes, mortality rates did not change at maturity. Ovarian weight and ovarian somatic index values were not significantly different between females from two acid and two circumneutral lakes. Values of fecundity, ova dry weight, testicular weight, and testicular somatic index of fish in acid lakes were either significantly greater than or equal to values in white sucker from circumneutral lakes. Results are discussed within the context of life history theory.

Comparativement aux meuniers noirs (*Catostomus commersoni*) de deux lacs à pH presque neutre (pH de 6,30 et 6,35), les meuniers noirs de trois lacs acides (pH de 4,90, 5,56 et 5,58) atteignaient fréquemment la maturité à des âges et des tailles plus élevés et présentaient des périodes reproductives plus courtes. La durée des périodes reproductives présentait une corrélation positive avec le pH des eaux du lac tant chez les femelles ($r = 0,97$) que chez les mâles ($r = 0,85$). Dans les lacs acides, les taux de mortalité élevés coïncidaient avec l'apparition de la maturité sexuelle tandis que, dans les lacs à pH presque neutre, les taux de mortalité ne variaient pas au moment de la maturité. Le poids des ovaires de même que l'indice somatique ovarien ne différaient pas de façon significative entre les femelles des deux types de lacs. Les valeurs de fécondité, le poids sec des oeufs, le poids des testicules et l'indice somatique testiculaire des poissons des lacs acides étaient significativement plus élevés ou égaux à ceux notés chez les poissons des lacs à pH presque neutre. Les auteurs traitent des résultats obtenus dans le contexte de la théorie du cycle vital.

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Abundance and biomass of white sucker (*Catostomus commersoni*) populations have been substantially reduced in acid lakes (Beamish and Harvey 1972; Beamish et al. 1975; Sun and Harvey 1986) or are much smaller than those in circumneutral lakes (Harvey 1982; Trippel and Harvey 1987). A characteristic of some of these depauperate populations is the low proportion of individuals older than 5 yr (Harvey 1980, 1982). Whether the strain of sexual maturation in suckers in acid lakes can cause an abnormally short adult life span has not been investigated, although there is some evidence that maturation-induced mortality occurred in brown trout (*Salmo trutta*) (Rosseland et al. 1980) and brook trout (*Salvelinus fontinalis*) (Frenette and Dodson 1984).

Another feature of some low-density white sucker populations in acid lakes is missing year-classes of young fish (Beamish and Harvey 1972; Harvey 1982; Mills 1984). Most often the cause of missing year-classes in this species has been cited as spawning failure (Beamish and Harvey 1972) or poor survival of fry (Mills 1984), but as yet there has been no report that oogenesis and spermatogenesis in suckers of acid lakes are at less productive levels than those of circumneutral lakes.

The objectives of this study were to determine whether age and size at onset of maturity, the length of the reproductive life span, and gonadal production in white sucker were related to pH in five study lakes.

Methods

Five lakes in south-central Ontario were chosen on the basis of lake morphometry and water chemistry (Table 1; Trippel and Harvey 1987) for study of the reproductive biology of white sucker. All lakes were deep (mean depth 8.4–18.6 m, maximum depth 25.0–38.0 m); shallow lakes were omitted, as white sucker abundance and growth has been shown to be different between shallow and deep lakes (Trippel and Harvey 1987). Three lakes were acid (mean annual pH 4.90–5.58) and two were circumneutral (mean annual pH 6.30 and 6.35). pH's of integrated water samples were determined by the Ontario Ministry of the Environment, Dorset, except for the integrated pH of George Lake which was measured using a Hydro Lab Surveyor or System 8000 (Hydrolab, Austin, TX). The hypolimnetic pH's in the three acid lakes ranged between

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TABLE 1. pH, location, and physical characteristics of the study lakes.

Lake	pH	North latitude	West longitude	Maximum depth (m)	Mean depth (m)	Surface area (ha)	Volume (10^6 m^3)
George	4.90	46°02′	81°24′	36.6	18.6	147.9	25.53
Chub	5.56	45°13′	78°59′	27.0	8.9	32.2	2.85
Crosson	5.58	45°05′	79°02′	25.0	8.4	56.8	4.77
Bigwind	6.30	45°03′	79°03′	32.0	10.7	111.1	11.80
Red Chalk	6.35	45°11′	78°57′	38.0	14.2	56.9	8.08

TABLE 2. Range in fork length of white sucker age-classes 1 and 2 yr collected from five lakes during sampling periods 1, 2, and 4. Sample sizes in parentheses.

Lake	Range in fork length (cm)	
	1 yr old	2 yr old
George	11.8–17.4 (2)	23.5–30.5 (31)
Crosson	16.3–19.7 (3)	20.3–28.4 (7)
Chub	16.6–18.7 (4)	21.5–28.3 (53)
Bigwind	14.3–19.4 (33)	20.2–27.8 (48)
Red Chalk	16.2–19.2 (11)	21.9–28.5 (12)

5.0 and 5.4 whereas the hypolimnetic pH's in the circumneutral lakes were approximately pH 6.5 (Harvey 1980; LEWG 1980; R. Reid, Ontario Ministry of the Environment, pers. comm.). Aluminum and manganese concentrations were higher in the acid lakes (Trippel and Harvey 1987). Fish from each lake were collected during four intervals: period 1, April 26 – May 24, 1981; period 2, June 7 – 27, 1981; period 3, August 17 – September 30, 1981; and period 4, May 4 – 19, 1982. Periods 1 and 4 coincided with annual spawning. Fish were captured in overnight sets of experimental gill nets (panels of 51- , 64-, 76-, and 89-mm stretched mesh), gill and trammel nets (64, 76, 89 mm), and fyke and trap nets. Sucker exposure to hypolimnetic acid conditions occurred, since nets set in the deepwater zone of acid lakes captured suckers.

Fork length (±0.1 cm), somatic weight (±5–10 g), sex, and gonadal stage of development (Trippel 1984) were recorded for each fish during all sampling periods. Pectoral fin rays and scales were removed for age determination from fish of each population (Beamish and Harvey 1969). Scales plus size-class distributions (Table 2) were used to aid in identifying the first annulus in fin-ray sections (Beamish 1973).

A formula developed by Abrosov (1969) and modified by Lysack (1980) was used to determine mean weighted age at the onset of first maturation (Z_{age}) for each sex in each population:

$$Z_{age} = \frac{A_1K_1 + A_2(K_2 - K_1) + A_3(K_3 - K_2) + A_n(K_n - K_{n-1})}{K_1 + (K_2 - K_1) + (K_3 - K_2) + (K_n - K_{n-1})}$$

where A = age (years) and K_n = percent of mature fish in the nth age-class. Lysack's formula also was used to determine the mean weighted fork length at onset of maturation. This was done by subdividing the catch into 2-cm size-classes, and instead of using Lysack's A to represent age, we used it to represent a fork length size-class, for example 20.0–21.9 cm. Fish used in these analyses were captured during periods 1, 2, and 4. Fish sampled during period 2 that were maturing for the first time were thus immature during period 1 and were represented as immature in the formula. Mean weighted age at the onset of sexual maturity was used rather than age at which 50% maturity occurred. The former approach provided appropriate weighting of all ages of a population. The same reasoning applied for its use in determining size at maturity. Reproductive life span (RLS) of an average fish in the catch was determined according to Abrosov (1969) by subtracting the value of Z_{age} from the mean age of the catch ($\bar{x}_{age}$). Annual mortality rates for each sex were determined from age frequency tables of total catch data using the formula $1 - (N_{t+1}/N_t)$ (Ricker 1975) where N_t represents number of fish in age-class t and N_{t+} represents number in the subsequent age-class. Shortcomings of this method are that it assumes an equal initial number of two broods and subjection to similar mortality rates at corresponding ages. Annual mortality rates were calculated for each of the 2 yr prior to and 2 yr after the mean age at maturity (rounded to the nearest year).

Weight of ovaries (±0.1 g), ovarian somatic index (OSI = (weight of ovaries/somatic weight) × 100), fecundity, and dry weight of 100 ova were determined for each gravid female that lacked evidence of ova release collected during periods 1 and 4. Fecundity was determined by drying ovaries (Bouin's preservative) at 80°C until constant weight was attained (2–3 d). Ovaries were teased apart and connective tissue removed. Fecundities of the left and right ovaries were determined separately. Three samples of ova were removed from each ovary and weighed (±0.001 g); each sample constituted about 1.5% of the dry weight of the ovary. Fecundity estimates were calculated by the following operation: (number of ova in dried sample/dry weight of sample) × dry weight of entire ovary. The estimates of the three samples per ovary (within 5% of each other) were averaged to yield the fecundity per ovary. The fecundity estimate of the entire gonad was the sum of the fecundity estimates for the left and right ovaries.

The mean dry weight of a mature ovum in each ovary was determined by averaging the three ovum dry weight values calculated in each of the samples used in determining its fecundity. To compensate for any ova dry weight differences between the left and right ovaries, the mean ovum dry weight value for each of the left and right ovaries was multiplied by the proportion (as a percentage by dry weight) that each ovary composed of the total ovarian weight. The mean ovum dry weight for each female was the sum of these values for the left and right ovaries. The mean dry weight of 100 ova per mature female was obtained by multiplying this value by 100.

Weight of testes and the testicular somatic index (TSI = (weight of testes/somatic weight) × 100) was calculated for each male that was mature (collected during periods 1 and 4) or undergoing spermatogenesis (period 3) but lacked evidence of spermatozoa release. There was no significant difference in testes weight or TSI between males collected during these periods (ANOVA, $P > 0.05$), and therefore, data were pooled for each population (Trippel 1984).

TABLE 3. Age at onset of maturation (Z_{age}) (Lysack 1980), fork length at onset of maturation (Z_{FL}), mean age of the catch ($\bar{x}_{age}$), and reproductive life span (RLS = $\bar{x}_{age} - Z_{age}$) (Abrosov 1969) for each sex of white sucker in five lakes. Sample sizes in parentheses.

	Females				Males			
Lake	Z_{age} (yr)	Z_{FL} (cm)	$\bar{x}_{age}$ (yr)	RLS (yr)	Z_{age} (yr)	Z_{FL} (cm)	$\bar{x}_{age}$ (yr)	RLS (yr)
George	4.4 (88)	34.8	3.9 (120)	−0.5	3.5 (67)	30.9	4.5 (82)	1.0
Chub	2.8 (68)	28.6	3.6 (60)	0.8	1.8 (35)	23.4	3.4 (55)	1.6
Crosson	4.1 (48)	34.5	6.3 (75)	2.3	3.5 (31)	31.5	5.2 (44)	1.7
Bigwind	1.4 (154)	16.5	4.7 (182)	3.4	1.3 (52)	14.6	4.0 (68)	2.8
Red Chalk	3.1 (79)	26.7	7.1 (94)	4.0	2.3 (43)	22.4	7.4 (57)	5.1

Comparisons between the gonadal characteristics of the five populations were based on a single fork length size-class for each sex, as reproductive output varies with fork length in fishes (Bagenal 1967; Healey and Nicol 1975). These size-classes were 37–47 cm in females and 34–40 cm in males. The absence of gravid fish over a broad size range precluded calculation of regression equations between body size and gonadal characteristics for the purpose of interpopulation comparisons.

Single classification analysis of variance (GLM-ANOVA, SAS 1982) was used to determine if significant differences ($P < 0.05$) occurred between fish used to represent the gonadal characteristics of each population. For attributes where significant differences occurred, the Duncan's multiple range test (GLM-DUNCAN, SAS 1982) was used to determine which populations differed from one another. Data were log transformed to ensure that the variances were homogeneous (F_{max} test, $P > 0.05$) and because fork length and fecundity form a linear relationship after log transformation (Bagenal 1967; Healey and Nicol 1975). Pearson product–moment correlation coefficients were determined (CORR, SAS 1982) between reproductive life span for each sex in the populations and pH of the respective lakes.

Results

Onset of Maturation and Reproductive Life Span

Female white sucker matured later and at larger sizes than males in each population (Table 3). Onset of maturity in females of acid lakes tended to occur at older ages than those of females in circumneutral lakes. Length of female RLS was positively correlated with pH in the five lakes ($r = 0.97$, $P < 0.05$). Females in circumneutral lakes had RLS's 1.1–4.5 yr longer than females in acid lakes. The high RLS in each of the two circumneutral lakes occurred as a result of different life history characteristics. The high RLS in Bigwind Lake females occurred despite the relatively low mean age of the sample. This resulted from the early onset of maturation which was 1.5 yr lower than that of any of the other four populations. In Red Chalk Lake, female RLS was the highest of the five lakes. This was due to females of Red Chalk Lake origin having the highest mean age plus an intermediate age at onset of maturation.

Low female RLS in the two acid lakes George and Chub mainly occurred because of the low abundance of old fish in these lakes and their relatively high ages at maturity. Females from acid Crosson Lake also matured at a relatively old age. However, the higher mean age of the catch of Crosson Lake females (versus the other two acid lake populations) resulted in a higher RLS for Crosson Lake females. Fork lengths of females at onset of maturity in acid lakes were up to 2.1-fold larger than females in circumneutral lakes (Table 3). During the 2 yr preceding onset of maturity, annual mortality rates were generally very low for females of both acid and circumneutral lakes (Table 4). Mortality became very high in females of all three acid lakes during the 2 yr immediately after maturity, reaching between 66 and 100% by the second year; these postmaturation mortality rates were substantially higher than those for females of circumneutral lakes.

Male RLS, as in females, was positively correlated with lake pH ($r = 0.85$, $P < 0.05$). Males in circumneutral lakes had RLS's 1.1–4.1 yr longer than males in acid lakes (Table 3). Male suckers of acid lakes George and Crosson matured at the oldest ages among the five populations, which resulted in low RLS's for males of these lakes. Males from acid Chub Lake matured earlier than George and Crosson Lake males but died younger, resulting in a low RLS. Fork lengths of males at onset of maturity in acid lakes were up to 2.2-fold larger than those of males in circumneutral lakes. Mortality of males in acid lakes during the 2 yr postmaturation was much higher than during the 2 yr prematuration whereas in the circumneutral lakes, male white sucker showed no substantial increase in postmaturation mortality (Table 4).

Gonadal Production

Ovarian weight and OSI in females ranging from 37 to 47 cm fork length did not differ significantly among two acid and two circumneutral lakes (Table 5). Fecundities in fish from acid lakes either were significantly higher or equal to fecundities of white sucker from circumneutral lakes. Dry weights of 100 ova of females from Crosson Lake were significantly greater than those of females from any of the other populations.

Testicular development in white sucker was compared between fish from two acid lakes and one circumneutral lake within the size range 34–40 cm fork length (Table 5). Males from these three lakes did not differ significantly in fork length and somatic weight, but fish from the two acid lakes were significantly younger. Despite George Lake males being less than half the age of Red Chalk males, the George Lake males had significantly heavier testes (1.4-fold) and higher TSI's than males from Red Chalk Lake. Testes weight and TSI values of Crosson Lake males did not differ significantly from males of George or Red Chalk lakes.

Discussion

In the acid lakes, mortality rates for white sucker increased at sexual maturity, even though these fish were older and larger

TABLE 4. Annual mortality rates for female and male white sucker for five lakes c
Below each mortality rate is the age-class and the number per age-class. Zero v
and N/A indicates that no calculations were possible because fish matured at a

	Females		
	Prematuration		Postmaturat
Lake	−2 yr	−1 yr	+1 yr
George	0.00 II(25)−III(38)	0.45 III(38)−IV(21)	0.24 IV(21)−V(16)
Chub	0.00 I(1)−II(16)	0.00 II(16)−III(26)	0.50 III(26)−IV(13)
Crosson	0.00 II(4)−III(19)	0.00 III(19)−IV(19)	0.58 IV(19)−V(8)
Bigwind	N/A	N/A	0.00 I(3)−II(23)
Red Chalk	0.00 I(0)−II(16)	0.00 II(16)−III(7)	0.00 III(7)−IV(10)

TABLE 5. Gonadal characteristics of female (37−47 cm FL) and male (34−40 cm Fl
with no letters following are not significantly different (ANOVA, $P > 0.05$), and
mature fish in these size-classes were caught in Chub Lake (both sexes) and Bigwinc

	Females				
Lake	Fork length (cm)	Somatic weight (g)	Age (yr)	Ovarian weight (g)	Fecundity
George	42.5±1.8	1129±170	7.1±1.8	162.3±30.8	33 576±5438 a
Crosson	42.8±1.6	1120±152	8.6±2.6	187.2±36.0	28 696±4870 ab
Bigwind	41.5±3.4	981±258	9.4±3.4	148.2±52.2	25 292±4134 b
Red Chalk	41.5±0.8	974±60	9.7±1.2	153.0±14.2	29 600±3064 ab

e lakes determined from catch data for 2 yr preceding and 2 yr following age at onset of maturation (Z_{age}). . Zero values indicate that a greater number of fish were caught in the N_{t+1} age-class than the N age-class, red at a very early age.

	Males			
tmaturation	Prematuration		Postmaturation	
+2 yr	−2 yr	−1 yr	+1 yr	+2 yr
0.69	0.00	0.36	0.21	0.46
V(16)−VI(5)	II(17)−III(22)	III(22)−IV(14)	IV(14)−V(11)	V(11)−VI(6)
1.00	N/A	0.00	0.00	0.83
V(13)−V(0)		I(1)−II(7)	II(7)−III(36)	III(36)−IV(6)
0.88	0.00	0.00	0.73	1.00
V(8)−VI(1)	II(14)−III(14)	III(14)−IV(5)	IV(15)−V(4)	V(4)−VI(0)
0.00	N/A	N/A	0.00	0.04
II(23)−III(54)			I(2)−II(25)	II(25)−III(24)
0.00	N/A	0.00	0.00	0.00
IV(10)−V(11)		I(0)−II(3)	II(3)−III(4)	III(4)−IV(5)

40 cm FL) white sucker in several study lakes. Mean ± 95% confidence limits are listed. Values in columns 05), and values within columns not having a common letter differ significantly (DMR test, $\alpha = 0.05$). No Bigwind Lake (males).

					Males				
ty	Dry weight of 100 ova (mg)	OSI	*n*	Fork length (cm)	Somatic weight (g)	Age (yr)	Testicular weight (g)	TSI	*n*
38 a	186±8 b	14.3±0.8	8	36.3±1.0	697±68	3.6±0.6 c	51.2±10.8 a	7.6±1.4 a	12
70 ab	234±14 a	16.5±1.2	11	37.6±1.0	745±90	4.8±1.6 b	42.6±7.6 ab	5.8±0.8 ab	11
34 b	203±48 b	14.9±3.4	5						
54 ab	197±10 b	15.6±1.0	26	36.5±0.8	647±42	8.5±1.2 a	36.0±6.0 b	5.5±0.6 b	14

at first maturity than were white sucker from circumneutral lakes; the latter showed no change in mortality rates with onset of maturity. Two studies have reported results consistent with increased mortality of adult fish in acid lakes. Prior to a massive fish kill in Lake Tveitvatn of the Tovdal River, Norway, five year-classes of mature brown trout were present; the first year following the fish kill, only two adult year-classes were found and only juveniles were captured in later years (Rosseland et al. 1980). Female brook trout of acidified Lac Tantaré, Quebec, experienced a high rate of mortality when they reached a size at which 50% were mature, even though size at maturity was much larger than that normally found in brook trout (Frenette and Dodson 1984).

The brief reproductive life span in acid-lake suckers was caused by delayed maturity plus short life span. Length of reproductive life span of female and male suckers ranged from −0.5 to 1.7 yr for five of the six values (Table 3). These five low values are an indication of population instability based on recommended positive values for eastern European species (Abrosov 1969) and the minimum 1.5 spawnings required for replacement of lake whitefish (*Coregonus clupeaformis*) in Lake Ontario (Christie 1972; OMNR 1983). The higher RLS (2.3 yr) of Crosson Lake females was surprising, since sampling in 1979 did not yield many suckers greater than age 5 (Harvey 1982). This higher value apparently was a function of several suckers older than 12 yr in the 1981–82 catches.

It was demonstrated previously that the acid-lake white sucker of this study had a large food supply per individual (Trippel 1984; Trippel and Harvey 1987). We showed that somatic weights of 4-yr-old suckers were much greater (1.6- to 2.1-fold) in the low-density populations of the acid lakes (catch per unit effort was 12–25% of that in circumneutral lakes) and this increased growth rate was correlated with food abundance. In other fishes, an adaptive response has been observed in heavily exploited low-density fish populations where removal of older fish was followed by faster growth of juveniles (Nikol'skii 1962; Healey 1980; Colby and Nepszy 1981), by decreased age at first maturity (Nikol'skii 1962; Diana 1983), and by increased recruitment (Healey 1980). Despite numerous white sucker removal programs during the last three decades, there has been no information on whether surviving white sucker displayed reproductive characteristics common to *r*-selection (Parker 1958; Johnson 1977; Holey et al. 1979; Henderson 1986). Evidence that low-density white sucker populations make such reproductive adjustments to high adult mortality was presented by McFarlane and Franzin (1980), who noted that relatively short-lived white sucker, apparently stressed by high zinc levels, exhibited a faster rate of growth and a lower age at first maturity in comparison with a population in a nearby unstressed lake. We can only speculate as to the absence of early maturity among fast-growing suckers in the acid lakes. For each year a fish delays maturity, it can allocate more of its energy to somatic growth. Thus, a fish will be larger in the subsequent year if it remains immature than if it matures. At a larger size, fish are more tolerant of acidic conditions (Robinson et al. 1976; Swarts et al. 1978), and the risk of mortality caused by the physiological stress of maturation may be reduced (Calow 1979; Bell 1980). Furthermore, fecundity increases exponentially with increasing fish length (Bagenal 1967). Therefore, delayed maturity under conditions of physiological stress would make possible a single, relatively large reproductive effort, prior to the high postspawning mortality. Physiological stress as a mechanism influencing fish life history traits has been identified previously, for example in relation to salinity (Stearns 1980).

White sucker in circumneutral Bigwind Lake, having shorter life spans and slower growth, matured at earlier ages and smaller sizes, consistent with life history theory (Stearns and Crandall 1984; Ware 1984). The low mortality, postmaturation, of the Bigwind Lake population permitted a level of iteroparity similar to that in the (circumneutral) Red Chalk Lake population with its much greater average longevity.

Weights of ovaries and OSI were similar among suckers from acid and circumneutral lakes despite the faster somatic growth rates of acid-lake suckers. In contrast, fast-growing fish of exploited populations have a relatively greater reproductive output: plaice (*Pleuronectes platessa*) (Bagenal 1966), lake trout (*Salvelinus namaycush*), and lake whitefish (Healey 1978). Physiological stress in white sucker during oogenesis could be affecting reproductive output, as Beamish et al. (1975) reported that adult females in George Lake had abnormally low concentrations of plasma calcium coincident with a high incidence of ovarian resorption. Additional evidence of stress is that cadmium was accumulating in the liver of George Lake white sucker at three times the rate that occurred in suckers of circumneutral Red Chalk Lake (Bendell-Young et al. 1986).

Reduced egg size did not occur in acid-lake fishes, but rather, Crosson Lake females had significantly heavier mean ovum dry weights than the other populations. Larvae emerging from larger eggs grow faster and survive better than those emerging from smaller eggs (Bagenal 1969; Pitman 1979), and as white sucker prolarvae will not tolerate pH 5.0 (Trojnar 1977), larger size may be enhancing survival of larval suckers in acid waters.

Spermatogenesis in natural fish populations in relation to lake acidification has not been reported on previously. Testicular weight and TSI were 1.4-fold greater in fish from George Lake than in those from circumneutral Red Chalk Lake. Perhaps a more positive reproductive response occurred in fast-growing males than in females because less energy is required for testicular than ovarian development (TSI is ~50% of OSI, Table 5). Also, males accumulated all of their testicular tissue during the summer when somatic growth was fast, in contrast with females which underwent oogenesis during the period of slow somatic growth in autumn and early spring (Lalancette 1975, 1976; Trippel 1984). Thus, oogenesis may demand more energy from stored reserves. Spring spawning female northern pike (*Esox lucius*), with a maturation schedule similar to white sucker, deposited 6- to 18-fold more energy into the gonads than did male pike (Diana 1983).

In summary, probable causes of the low densities of white sucker in acid versus circumneutral lakes were (1) first onset of sexual maturity at older ages, (2) higher incidence of mortality at and/or following maturation (1 and 2 resulting in very brief reproductive life spans), and (3) constant ovarian production independent of the fast somatic growth rate of suckers in acid lakes.

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A Model for Comparing Fish Density Estimates from Seine Catches and from Echo Integration

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A model for comparing acoustic and nonacoustic fish density values yields estimates for the ratio of the biases and the variances for the two sets of density measurements. The model compares seine catches and echo integration values. The correlation between the two sets of measurements is 0.98. The data seem to be well described by the model. A discussion is included of the role such comparisons might play in research or fisheries management, for fish behavior studies, for comparison of the relative precision of each technique, and for selecting individual measurements which should be duplicated.

Un modèle servant à la comparaison des densités du poisson obtenues à l'aide de méthodes acoustique et non acoustique a généré des estimations du rapport entre les biais et les variances des deux séries de quantifications de la densité. Le modèle compare les valeurs obtenues des relevés à la senne et par intégration échographique. La corrélation entre les deux séries de données, qui semblent être bien décrites par le modèle, se situe à 0,98. On présente aussi une discussion du rôle de telles comparaison dans la recherche, la gestion des pêches, les études de comportement du poisson, la précision relative de chaque technique et le choix des mesures individuelles qui devraient être répétées.

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Herring are fished by many nations around the world. Echo integration estimates of herring density have become standard information used by some nations in the management of their fisheries. The measurement requires a stable, calibrated echo sounder employing a 20 log R time-varied gain plus some type of further signal processing to perform the integration of the measured signals (Forbes and Nakken 1972; Burczynski 1982; Johannesson and Mitson 1983). The resulting biomass density values are used to arrive at abundance estimates. The acoustic technique is particularly valuable because estimates of biomass can be obtained quickly and are therefore useful for in-season management (Trumble et al. 1982).

A calibrated echo integration system was used to collect the acoustic data (Kieser et al. 1987). Biomass per integrator output unit can be determined either from measurements of caged fish (Edwards and Armstrong 1983) or from in situ measurements of target strength (Ehrenberg 1983a, 1983b; Lindem 1983) plus equipment calibration. Accuracy and precision of biomass estimates also depend on the distribution and behavior of the fish. Olsen et al. (1983) found that several schooling fishes exhibited strong avoidance behavior at the approach of a large (600 t) survey vessel. The avoidance behavior was more pronounced for fish near the surface and for large vessels underway at high speed than it was for deeper fish and small vessels at low speed. The more pronounced reaction resulted in a 40–90% decrease in echo integrator output at the moment of vessel passage. Consequently, a biomass estimate obtained via a hydroacoustic survey conducted from a large vessel could be very biased.

A given population of fish may not exhibit this type of behavior at all times. When possible, it is prudent to compare estimates of biomass per unit area derived by hydroacoustic techniques with concurrent estimates derived by independent methods. We have developed a stochastic model to compare two types of fish density measurements. We feel that this model would be useful to anyone comparing an acoustic with either another acoustic or a nonacoustic technique (Kieser et al. 1987).

The requirements of the model have come from our experience with fish abundance measurements. We wanted a simple, linear model with few, physically meaningful parameters. At the same time, the model should describe the unique features of the measurement. The comparison must cover a wide range of densities if results are to be applied to typical field situations. This density scope may be especially important for herring which we have observed to cover a density range of ~1000:1.

We used our model to analyze a comparison of acoustic and purse-seine herring density estimates. The results of the analysis yield estimates of the ratio of the biases and the variances in addition to the test for a linear relationship between the two types of measurements. We feel that the variances are typical of actual field work with acoustic and net gear. Here, as in most cases, the true fish density is never known.

Since acoustic measurements are often accompanied by some type of net catches for species identification purposes, a means of combining both types of data could be usefully employed to enhance fish surveys. These comparisons may be useful to determine the extent to which fish can avoid gear such as trawls, etc. (Robinson and Barraclough 1978). In contrast

with caged fish experiments, our study involves field measurements using commercial fishing gear.

Materials and Methods

The Model

The following ideas provide the background for the mathematical model. Our experience with echo integration data indicates that a multiplicative error term is more appropriate for surface density estimates than an additive error term. (For example, a relative error of 25% represents a multiplicative error, while ±500 kg represents an additive error.) We feel that a stochastic model is required and that a mean density estimate is meaningful over some localized area. Within this "locally uniform" density region the surface density estimates can be regarded as a random variable with well-defined mean and variance. An important characteristic of the model is that both sets of observations, acoustic and seine, are related to the same fish density distribution, which itself is never actually known. Finally, we wanted a simple, linear model with few, physically meaningful parameters. With these ideas in mind we developed the following model to compare the acoustic and seine data.

During each 1-min period, a fish density is sampled by the acoustic beam and yields the ith measurement of the surface density. For a region of uniform density, we make several acoustic measurements, each measurement subscripted by i to indicate measurement number and j to indicate corresponding density region. Our model assumes the following relation between the fish density and the measured surface densities:

$$(1)\quad x_{ij} = \alpha\rho_j \exp(\sigma\epsilon_{ij})$$

where x_{ij} is the ith acoustic measurement of surface density from fish density j, α is the dimensionless acoustic bias term, $\rho_j \exp(\sigma\epsilon_{ij})$ represents the fish density distribution with mean ρ_j and variance σ^2, and ϵ_{ij} is the standard normal deviate. In our notation, Greek letters will be used to delineate unobservable distribution parameters and Roman letters will be used for observed measurements and sample estimates of distribution parameters. The subscript i has a range of 1 to m, while j has a range of 1 to n. Note that a "uniform density" region is lognormally distributed and is characterized by constant ρ_j and σ. The local fish density does not have to be lognormal; any distribution with a multiplicative error term could have been used. However, we have found lognormal distributions to give an adequate description of observations from "locally uniform" density regions, and this assumption greatly simplifies the subsequent calculations (Kieser et al. 1987).

The seine measurements are related to the fish density as

$$(2)\quad y_j = \beta\rho'_j \exp(\tau\epsilon'_j)$$

where y_j is the seine measurement of surface density from fish density j, β is the dimensionless seine bias term, $\rho'_j \exp(\tau\epsilon'_j)$ represents the fish density distribution with mean ρ'_j and variance τ^2, and ϵ'_j is the standard normal deviate. The x's and y's in eq. (1) and (2) represent the two sets of measurements we want to compare. We have assumed that both measurements are proportional to the fish density, but with different bias and error terms.

For our experiment, several acoustic measurements are compared with each seine catch; consequently, we wish to reduce the m acoustic measurements of fish density j to one average measurement so as to have a one-to-one correspondence between x and y. This step is accomplished by taking the arithmetic average of the acoustic observations:

$$(3)\quad \bar{x}_j = 1/m \sum_{i=1}^{m} x_{ij} \approx \alpha\rho_j \exp(\sigma/\sqrt{m}\,\epsilon_j)$$

where we have used the fact that for $\sigma \ll 1$ the arithmetic mean of m independent observations from a lognormal distribution is approximately lognormal with variance σ^2/m. This approximation can be verified easily by a first-order Taylor series expansion of a lognormal random variable. (This approximation is quite good for $\sigma = 0.2$, which is representative of the present case.) Usually for lognormal distributions the geometric mean is used. We have chosen to use the arithmetic mean in eq. (3) because a population estimate for the herring would be proportional to the expection value of the observed surface densities. We note that

$$E\{\bar{x}_j\} \approx E\{x_{ij}\}$$

where $E\{\}$ is the expectation operator, so that the population estimates resulting from either $\bar{x}_j$'s or x_{ij}'s will be equal.

We now wish to impose the following constraint on eq. (2) and (3):

$$(4)\quad E\{\rho_j \exp(\sigma/\sqrt{m}\,\epsilon_j)\} \approx E\{\rho'_j \exp(\tau\epsilon'_j)\}.$$

This constraint requires the actual fish densities sampled by the acoustic and seine measurements to be equal. The effect of this constraint on these equations is to relate the parameters ρ_j, ρ'_j, σ, and τ so that they are no longer all independent.

If $\sigma/\sqrt{m} \neq \tau$, then eq. (4) demands $\rho_j \neq \rho'_j$. However, if $\sigma/\sqrt{m}$ and τ are both ≤ 0.5, then $\rho_j \approx \rho'_j$ and the approximate equality of eq. (4) holds. We have chosen this set of constraints for eq. (2) and (3) because it greatly simplifies further calculations.

We now estimate the ratio of acoustic and seine bias terms by taking the natural logarithms of eq. (2) and (3), after equating ρ_j and ρ'_j:

$$w_j = \ln \bar{x}_j = \ln \alpha + \ln \rho_j + \sigma/\sqrt{m}\,\epsilon_j$$

$$z_j = \ln y_j = \ln \beta + \ln \rho_j + \tau\epsilon'_j.$$

We now have a set of equations that are linear with respect to the parameters of interest. We define the difference of w and z to be

$$(5)\quad d_j = z_j - w_j = \ln \beta - \ln \alpha + \tau\epsilon'_j - \sigma/\sqrt{m}\,\epsilon_j$$
$$= \ln(\beta/\alpha) + \tau\epsilon'_j - \sigma/\sqrt{m}\,\epsilon_j$$
$$= \delta + \eta\epsilon''_j$$

where $\eta\epsilon''_j$ is normally distributed with mean 0 and variance $(\tau^2 + \sigma^2/m)$. Thus, we expect the d_j's to be normally distributed with mean δ and variance η^2. This implies that $\ln(\bar{x}_j/y_j)$ has a constant value with random scatter about this value due to the combined error terms of both variables. Since eq. (5) has reduced to a simple expression, the evaluation of the sample estimate for the expectation value of the mean and variance is straightforward. We use the maximum likelihood estimate

$$(6)\quad \bar{d} = \frac{\sum_{j=1}^{n} d_j}{n}$$

for δ and

$$(7)\quad s_d^2 = \frac{\sum_{j=1}^{n}(d_j - \bar{d})^2}{(n-1)}$$

for η^2. These two equations evaluate the main parameters of the model.

Secondary parameters of interest in the model are the relative values of the variances σ^2 and τ^2. The x's give us the opportunity to get

$$s_j^2 = \frac{\sum_{i=1}^{m}(x_{ij} - \bar{x}_j)^2}{(m-1)}$$

which yields n independent estimates of σ^2. Since

$$E\{s_j^2\} = \sigma^2$$

we now get a point estimate for σ^2 by

$$(8)\quad s_p^2 = \frac{\sum_{j=1}^{n} s_j^2}{n}.$$

Once we know σ, we can estimate τ using the definition of η by

$$(9)\quad s_t^2 = s_d^2 - s_p^2/m.$$

The confidence interval for δ is calculated in the standard way using critical values of the t distribution, while the confidence intervals for η and σ use critical values of the χ^2 distribution (Sokal and Rohlf 1969).

Note that the following implicit assumptions have been made during the discussion of the model. First we have assumed that every ϵ_{ij} and ϵ_j' are independent, i.e. no serial correlations among a series of surface density estimates. Second we have assumed that COV $(\epsilon_{ij}, \epsilon_j') \approx 0$ so that this term has been ignored in the mathematical development of the model. We feel that these assumptions are realistic for our data. Unfortunately, the paucity of our observations prevents an examination of this question. However, in a similar study with many more observations (Kieser et al. 1987), we have tested and verified these two assumptions.

What are the limitations of this comparison model? It is meant to be a first-order description of the sampling process provided by echo sounding and seining. As such, we should be wary of putting undue emphasis on anything but the most basic results. The two most basic questions are: (1) Are the two sets of observations, w and z, linearly related? (2) What is the ratio of the two sets of observed densities? Unlike standard regression, our independent variable, the true fish density, is never observed. Our only method of testing the fit of the model is by the correlation coefficient of w and z. No goodness of fit statistic is produced.

Experimental Design

Before going into the field, we had conceived an experimental design which would allow a meaningful comparison of echo integration and seine density estimates. We hoped to find uniform herring densities over an area which was large compared with the area covered by the seine net. We planned to do the comparison at night when the typical behavior of the fish is to form a layer of reasonably homogeneous density somewhere in the water column. In addition, we wanted the acoustic measurement and the seine catch to be as concurrent as possible to avoid any bias due to time dependence of the fish distribution.

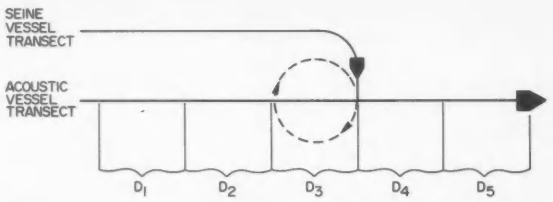

FIG. 1. Paths of the acoustic and seine vessels. The D's depict the distance along the vessel path represented by one acoustic surface density estimate. The figure presents a "snapshot" of the vessel locations 2 min after the measurements of D_3 has been made and just as the seine boat is about to start setting its net. The broken line represents the intended set location for the seine net.

When the experiment was carried out the acoustic data represented the mean surface density for 1 min of travel along a sounding transect. The vessel speed was ~6 knots; therefore, the surface density measurements were representative of a 185-m linear distance along the transect. The herring seine was 503 m long which equates to a diameter of 160 m if the net is set in a perfect circle. Therefore, each acoustic reading covered a distance roughly equivalent to the diameter of the seine net. However, the volume of water sampled by the acoustic beam and the net is quite different. Assuming a 10° half-angle for the acoustic beam, a travel distance of 185 m, highly overlapped adjacent acoustic sound cones, and a depth of 50 m, we calculate the acoustic volume as 0.8×10^5 m^3, while for the seine set in a perfect circle we get 10×10^5 m^3.

Our initial plan was to locate areas for which three to five successive acoustic readings gave a coefficient of variation on the order of 30%. This provided a working definition of an area of "uniform density." The corresponding experimental procedure is shown in Fig. 1. The seine boat was to follow the acoustic boat maintaining a distance of ~0.1 nmi astern and ~0.1 nmi to the port side. When an appropriate area was located, as indicated by approximately constant echo integration estimates ($x_1 \approx x_2 \approx x_3$), the seine boat could be given a 1-min advance signal of our intention to make a set. After the minute had elapsed, if the density was still homogeneous ($x_3 \approx x_4$), the set would be made in the region which the acoustic boat had completed sounding 2 min previously. The acoustic surface density measurements could be used to arrive at an estimate of the local herring density to compare with the seine catch.

In practice, much time was spent searching for herring concentrations of reasonably homogeneous density. As time passed and our patience waned, we compromised our definition of a "uniform density" distribution to require only two successive acoustic readings with a coefficient of variation of ~50%. Thus, we felt that the "uniform density" region would include only two or possibly three successive measurements.

The experiment was executed in January of 1982. A suitable concentration of Pacific herring (*Clupea harengus pallasi*) was located near Porlier Pass in the Strait of Georgia between Vancouver Island and the mainland of British Columbia, Canada. The fish distributions used in our comparison had a minimum depth of ~20 m, while the average depth of the sea floor was ~57 m. For some pairs of seine and acoustic measurements the fish schools extended to the sea floor, while for others they did not. The seine boat was a chartered commercial

seiner typical of the locally operating fleet. The net and method of setting were not altered from the common practice of commercial operation. Our echo integration system uses a 38-kHz echo sounder which transmits a 0.6-ms pulse at 1000 W with a repetition frequency of 2.1 Hz. A programmable digital echo integrator processes the detected signal and outputs relative backscattered signal strength per depth–time interval. The echo integration system and associated methods of data reduction which were used on the acoustic vessel are described in detail elsewhere (Kieser et al. 1987). An acoustic target strength of −32.0 dB/kg was used (Love 1971; Forbes 1975; Goddard and Welsby 1977; Traynor and Ehrenberg 1979; Edwards 1980; Forbes et al. 1980; Nakken and Venema 1983). We have used this same value for many species and did not want to change it unless we could get an in situ measurement of target strength.

Echo integration measurements estimate fish volume density (kilograms per cubic metre) as a function of depth and distance along the vessel's transect. The distance and depth increments can be quite small as compared with the diameter and depth of a seine net. By contrast, the seine estimates the average volume density within the volume enclosed by the net. We have found it convenient to transform both these measurements to surface density (kilograms per square metre).

The acoustic data provided surface density estimates directly from the output of the echo integration module; however, the seine catch had to be converted to similar measure. This conversion was accomplished by first estimating the surface area enclosed by the net and then estimating the weight of the fish contained in the net after it had been pursed. The area estimate was accomplished by tracing the outline of the net's cork line from the radar image immediately upon the joining of the seine boat and its net skiff. This tracing was later analyzed in the laboratory using a microcomputer, graphics board, and accompanying software to calculate surface area. The depth of the bottom varied between 42 and 66 m, while the stretched net depth was 95 m. Thus, we assumed that the fish within the net would be prevented from escaping under the net. The catch weight divided by the net surface area was used to represent the seine surface density estimate.

The second facet of the seine measurement involved estimating (hailing) the weight of the catch in the pursed seine. This estimate was made by the seine boat's skipper after the net had been drawn up as small as practical. In a separate subexperiment, described below, the skipper's estimate was compared with the actual landed weight of the catch to get some idea of his accuracy of hailing the catch.

Skipper's Catch Estimate

During the main experiment, logistic and conservation considerations prevented us from landing the seine-caught herring. This necessitated using the hailed catch for comparison with the acoustic values. The estimate was made by the seine boat's skipper, a man with many years of experience estimating catches in his nets. Seven sets were made followed by drawing up the pursed seine beside the vessel and recording the skipper's weight estimate. After he had guessed the catch weight, the herring were brought on board and stored in separate holds for each catch. When the fish were landed the weights in the various holds were measured on the cannery scales. These data were then used to determine the skipper's accuracy.

A log–log linear regression was performed on the estimated catch data using the SAS statistical analysis software (SAS Institute Inc. 1982). The log scaling was chosen because we felt that a multiplicative error was more appropriate than was an additive error. The measured weight was used as the independent variable and treated as thought it was without error. All observations fell within the 95% confidence interval around the regression line (Fig. 2). The analysis of variance results for the regression (Table 1) demonstrate a highly significant fit to the observed data. The mean of the absolute value of the residuals shows that, on average, the skipper's estimate differed by ~22% from the measured weight.

The seven catches represented in these data spanned a weight range from 6500 to 41 000 kg, a more restricted range than we expected to catch when comparing seine with acoustic data. Therefore, we treated the regression analysis as indicative of the skipper's accuracy. We did not use this regression to correct the hailed estimates from the main experiment.

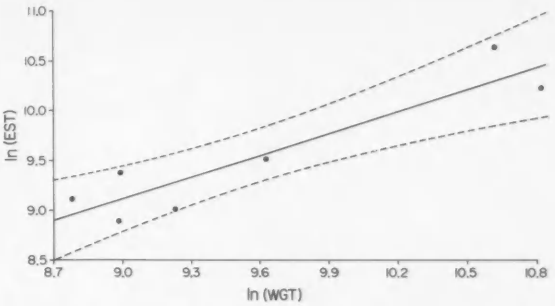

FIG. 2. Plot of the natural logarithms of the skipper's estimated weight versus the measured weight. The solid line represents the regression result, while the broken lines are the 95% confidence interval around the regression line.

TABLE 1. Test of significance and parameter estimates obtained from a log–log linear regression of estimated weight on measured weight.

Analysis of Variance

Source	df	Sum of squares	Mean square	F value	Prob. $> F$
Model	1	2.15	2.15	28.6	0.003
Error	5	0.38	0.08		
Total	6	2.53			

Parameter estimates

Intercept	Slope	Correlation coefficient	R^2	Mean residual
2.59 ± 1.30	0.73 ± 0.14	0.92	0.85	~0.22

Results

Our model gives a reasonable fit to the data. The experiment was carried out with a total of 11 seine sets useful for comparison with the acoustic values. Three seine sets were discarded because of some malfunction, e.g. the net being caught in a tide rip. Additional sets were made on either anchovie or on a mixture of herring and anchovie and were also discarded.

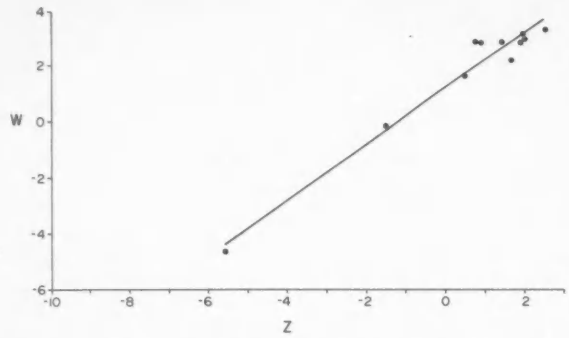

FIG. 3. Plot of the natural logarithms of the acoustic (w) and seine (z) surface density measurements. The observed values for the average of two acoustic readings and the corresponding seine value are represented by the discrete points. The line represents the $m = 2$, $n = 11$ model fit of the data. The correlation coefficient for w and z is 0.98.

TABLE 2. Parameter estimates for different combinations of acoustic and seine observations.

Number of observations		Parameter estimate			
m	n	$\bar{d}$	s_d	s_p	s_t
1	11	−1.176	0.515		
2	11[a]	−1.174	0.471	0.217[b]	0.445
3	11	−1.205	0.450	0.270	
3	11	−1.183	0.487	0.501	
5	11	−1.127	0.525	0.853	
2	10	−1.200	0.488	0.226	0.461
2	9	−1.186	0.515	0.154	0.504
3	10	−1.215	0.473		
3	9	−1.179	0.487		

95% confidence intervals for the $m = 2$, $n = 11$ case		
$\bar{d}$	−0.856	−1.489
s_d	0.329	0.827
s_p	0.154	0.368

[a]We believe the $m = 2$, $n = 11$ case to provide the best parameter estimates.

[b]The $n = 2$ estimate of σ is not rejected by Bartlett's test. We have used it to obtain estimates of τ.

The observed densities span almost four orders of magnitude (~0.004 to ~30 kg/m^2) and yet seem to remain linearly related with constant slope (Fig. 3). Correlation coefficients between the residuals (defined as $d_j - \bar{d}$) and w and between the residuals and z are −0.17 and 0.03, respectively, and are not significant at the 5% confidence level. We conclude that relative seine and acoustic densities are linearly related over a wide density range.

Equation (5) states that the d_j's should be normally distributed. We tested the $m = 2$, $n = 11$ d_j's for normality using the Shapiro–Wilk statistic, W (Shapiro and Wilk 1965). The resulting W was 0.933 with a probability of 0.457 of obtaining a smaller value of W from random data. Our conclusion is that the d_j's appear to be normally distributed.

How many acoustic and seine observations should be included in the model? Two of the observed values shown in Fig. 3 represent substantially lower densities than the other nine. It is legitimate to ask if these observations had greater than normal influence on the fit due to their leverage, i.e. distance to the mean of w, z. Parameter estimates from the model were made for several combinations of m and n (Table 2). It is reassuring to note that $\bar{d}$ and s_d remain relatively stable for all these combinations. The cases for which $n = 10$ or 9 represent the removal of one or both very low density points. It seems that these two observations have not had a large effect on the parameter estimates. (If one or both of these observations had had a large residual, their effect on the overall model would have been greater.) Consequently, we regard the $n = 11$ calculations as the best data set, since all seine observations are included. To chose a value for m, we performed a Bartlett's test for equal variance on the values we obtained for s_j for all $n = 11$ data combinations. Only the $m = 2$ case gave a B statistic less than the critical value. For all other values of m, the hypothesis of equal σ's for each of the 11 separate estimates was rejected. Therefore, we have chosen to use the $m = 2$, $n = 11$ paramater estimates rather than further complicate the model by introduction of additional parameters, i.e. a different σ_j in addition ρ_j for each "locally uniform" density.

Although the surface density ratio remains constant over a wide range, there is a significant difference in the absolute densities. The estimate of $\bar{d}$, −1.17, means that the absolute value of the acoustic measurements was approximately three times as large as the corresponding seine measurements. The individual d_j's varied from −0.5 to −2.1 for the data of Fig. 3. (Note that the model does not estimate α or β, only $\ln(\beta/\alpha)$).

A few results of lesser importance are also worth mentioning. Table 2 shows that $\tau > \sigma$ for all cases with $m = 2$. We would have expected $\tau < \sigma$, since the seine samples a volume roughly 10 times that of the acoustic beam. Obviously some additional mechanism must be involved to produce these results. One of these mechanisms is the error in the skipper's hailed estimates. Other sources, such as the error in the calculation of surface area covered by the set, etc., have not been assessed. Another point is that the model assumes that w and z are linearly related with a slope of 1. Our data are insufficient to use with a more complicated model which would allow the slope to vary. The interpretation for a model with slope not equal to 1 would imply a change with density of the relative efficiency between the two methods.

Discussion

The agreement of the surface density ratio over a range of ~1000:1 suggests that seine and acoustic density estimates measure the same property and that our model provides a reasonable description of the process. Our model assumes that both measurements are proportional to the true fish density. The fact that the true densities are rarely if ever known is typical. Comparisons similar to our study are a means of checking for possible problems with independent measurement methods. Caution is still required of too literal an interpretation of our results. A high correlation between w and z does not verify that they are correctly reflecting the true fish density, only that their relative estimates remain proportional. Although two independent and accurate fish density assessment methods would yield highly correlated results, the inverse cannot be implied. Correlation alone does not imply validity.

Acoustic population surveys usually employ some form of

net catches as a means of species identification of the acoustic targets. If carefully conducted, the net catches can yield fish density estimates as well as species information. Often the logistic considerations of a large fish population survey prevent the exact coordination of vessels. For those cases where such coordination is possible, the model presented here allows comparison of the density estimates between the two methods. We believe that our results are representative of the type of agreement achievable. The combination of two independent methods is potentially more powerful than either method in isolation. Once a linear relation has been established between the methods, departures from the expected relation might indicate measurements which need to be repeated or where different assumptions are required. Although the correlation does not acquire predictive status, it is useful for identification of potential problems. The combined data yields density verification, recognition of possible sources of trouble, as well as species identification of acoustic targets.

Our study should not be thought of as a type of calibration exercise. Calibration implies comparison of the observed value with the "true" value. Only for rare, self-contained systems such as caged fish, etc., will a measurement of the "true" value be possible. The end result of our experiment is an estimate of $\ln(\beta/\alpha)$ rather than estimates for α and/or β.

In general, relative estimates of fish density are subject to many fewer sources of error than are absolute estimates. This is brought into sharp focus by our work. Our relative densities had a correlation coefficient of 0.98, yet the absolute estimates differed by a factor of 3. Population abundance estimates resulting from the acoustic data would be three times as large as those based on the seine data. Does this discrepency seem reasonable in light of our present knowledge of acoustic and seine measurements? Possible sources of error influencing the bias terms α and β are examined below.

Both acoustic and seine surface density measurements will be influenced by errors from various sources. Three of these sources — measurement efficiency, fish behavior, and unique environmental influences — are common to both methods and hopefully represent the major sources of potential error. Measurement efficiency errors for acoustic data are contained in the uncertainty in the system calibration factor and the fish target strength. A careful study of our system calibration procedure revealed a range of 0.5−1.5 dB as a reasonable bound for this error (Kieser et al. 1987). Our target strength value of −32 dB/kg comes from surveys of many species of fish. We are unaware of any published target strength studies of Pacific herring; however, several studies have been made for Atlantic herring (*Clupea harengus harengus*). Edwards and Armstrong (1983) obtained a mean target strength during daylight of −32.5 dB/kg for caged herring of approximately the same size as ours. The nocturnal target strength was 2−3 dB/kg lower than the diurnal value. The total range in values was ~10 dB/kg. Halldorsson and Reynisson (1983) measured in situ target strengths at night. Their value of −34.8 dB/kg agrees well with the nocturnal value reported above. Studies by Buerkle (1983) indicate that this diel variation is likely due to the different mean orientation of the fish in daylight and darkness. These measured values show that there is substantial variation in herring target strength with time and that our assumed value is more likely to have been too high (by about 3 dB/kg) than too low. A +3 dB error in target strength causes a factor of 2 decrease in the measured surface density. Thus, our acoustic surface densities are more likely to be too low than too high from this source of error, producing an even larger difference between our acoustic and seine measurements. Target strength uncertainty is probably the largest single source of error for the acoustic measurements.

The influence of fish behavior has been investigated by Olsen (1979, 1980) and Olsen et al. (1983). By monitoring the measured fish density from a stationary echo sounder as a large vessel approached and passed nearby (<200 m), Olsen observed pronounced decreases in density (~90%) at the moment of passage. The response was greater for fish near the surface and for higher vessel speed. The vessels used in these experiments were about 20 times larger than our acoustic boat; however, the existence of a possible large source of error has been dramatically demonstrated. We have no evidence of or estimate for the influence of fish behavior on our measurements. Olsen's results would indicate that the observed density should be lower than the true density.

The unique environmental influences affecting acoustic data are such things as water temperature, currents, rolling motion of the boat's transducer, depth of the transducer, etc. For a temperature-stable modern transducer in light seas, the errors introduced by these sources are negligible and are usually ignored by most authors.

We now examine the same three sources of potential error for the purse seine measurements. The measurement efficiency errors for net catches are represented by the uncertainty in catchability and the skipper's hailed catch estimates. We believe that the errors associated with seine catchability are probably the single largest source of error for the net fish density estimates. Although several studies have been made of mechanisms for variability in trawl catches (e.g. Carrothers 1981), we have been unable to find similar published studies for purse seines. Mechanisms for variability of net catches can be identified; however, assessment of the associated variability is extremely difficult. In our study the seine was set over a continuum of fish, not over discrete schools. During a set, some fish could either swim out of the path of the vessel or into the partially closed net. This phenomenon could account for greater variability in the seine density estimates, but should only contribute to a bias if one mode of fish behavior was dominant. Acoustic observations can be accurately represented by a rigorous physical model of sound scattering. No analogous rigorous model exists for net catches, and therefore the assessment of variability is untenable. We are left with an unknown error for catchability of the seine plus our previous assessment of error for the hailed catch.

The influence of fish behavior on the seine estimate is similar to that for the acoustic measurements. The two boats were of similar size and maintained the same speed. The additional disturbance due to setting of the net has the potential to increase the avoidance response of the fish. We surmise that it is more likely to result in a lower fish density measured by the seine than by the acoustic vessel.

Unlike the acoustic measurement, the influence of unique environmental factors can make substantial differences in the seine catches. We have already mentioned our discarding of some seine catches because of obvious influences of tide rips, bottom configuration, etc. Undoubtedly there were instances in which the effects of current, unusual net performance, etc., were not detected. It is very difficult to achieve a repeatable "standard set" for a purse seine. Perhaps much of the error from this source will be represented in the associated variance term for the seine, rather than as a consistant error which would

affect the bias.

Our conclusions from the above consideration of sources of error for the individual bias terms α and β follow. Both measurement methods have the potential for a large bias. Many of the possible sources for this bias are difficult or impossible to measure. From our experience, we believe that the observed ratio of 3:1 for acoustic to seine density estimates is well within the bounds of what can be expected. We do not think that this situation can be improved significantly. For this reason, we feel that a time series of measurements of relative fish abundance rather than estimates of absolute abundance may be more useful to fisheries managers. Furthermore, the same measurement technique should be used each time, and when new techniques are introduced, considerable cross correlation should be undertaken before the new technique is adopted.

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Components Analysis of Instream Escapement Methods for Pacific Salmon (*Oncorhynchus* spp.)

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Escapement counts of Pacific salmon (*Oncorhynchus* spp.) have played a critical role in the development of fisheries science. We describe the components of instream escapement counts which are (1) an estimate of the number of fish in the stream at specific times, (2) a method for interpolation between visits to estimate total number of fish present at any time and (3) an instream residence time parameter to determine total number of fish that spawned for the entire run. Estimation of number of fish present at any time depends on species, observation method, stream habitat type, and observer experience. Our generalized model accounts for all of these factors in a biologically meaningful manner. Data were collected by five methods for three species of salmon which were counted past a weir; however, the number of fish present was unknown to observers. Counts for walking found, on average, 20% of fish present, for rafting 43%, for swimming 63%, for fixed wing 85%, and for helicopter 100%. The reliability of different methods as an index of abundance was similar, despite variation in the proportion of the fish observed by each method. Subsampling of specific stream sections provided a good index of abundance.

Les dénombrements de l'échappée de saumons du Pacifique (*Oncorhynchus* spp.) ont joué un rôle critique dans le développement de l'halieutique. Les auteurs décrivent les composantes du dénombrement de l'échappée en milieu fluvial, soit 1) une estimation du nombre de poissons présents dans le cours d'eau à des moments donnés, 2) une méthode d'interpolation entre les visites pour estimer le nombre total de poissons présents à tout moment et 3) un paramètre lié au temps de séjour en milieu fluvial pour déterminer le nombre total de poissons qui ont frayé pour toute la remonte. L'estimation du nombre de poissons présents à tout moment dépend de l'espèce, de la méthode d'observation, du type d'habitat fluvial et de l'expérience de l'observateur. Notre modèle généralisé tient compte de tous ces facteurs dans un contexte biologique significatif. Les données ont été recueillies selon 5 méthodes pour les trois espèces de saumons dénombrés à un barrage; toutefois, le nombre de poissons présents était inconnu des observateurs. Les observateurs à pied ont dénombré, en moyenne, 20 % des poissons présents, ceux en radeau 43 %, ceux à la nage 63 %, ceux à bord d'aéronef à voilure fixe 85 % et ceux en hélicoptère 100 %. La fiabilité des différentes méthodes à titre d'indice de l'abondance était semblable malgré les variations du nombre de poissons observés selon chaque méthode. Le sous-échantillonnage de certaines parties de cours d'eau a généré un bon indice de l'abondance.

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The unusual life history of Pacific salmon (*Oncorhynchus* spp.), which home to their natal streams, spawn in fresh water and die, has given these species a disproportionate role in the development of fisheries theory. The development of theory on harvesting policies for single stocks (Ricker 1958, 1963, 1973; Walters 1975; Walters and Hilborn 1976) or mixed stocks (Paulik et al. 1963; Hilborn 1976) was largely facilitated by this simple life history. Similarly, much of the earliest work on stock and recruitment (Shepard and Withler 1958; Ricker and Smith 1975) and stock structure (Larkin and McDonald 1968; Ricker and Smith 1975; Hilborn 1985) is due to the ability to readily estimate cohort sizes. The cohort sizes can be estimated because the fish spend the last part of their lives in streams where they can be counted. The ability to count the populations at the end of the life history has provided researchers of Pacific salmon with the key ingredient that those investigating pelagic and demersal species are now acquiring with the use of virtual population analysis.

The need to understand the reliability of escapement data has been accentuated by the recent discovery that unbiased escapement estimates, which vary about the true escapement, produce very seriously biased estimates of optimum harvest rate and

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optimum escapement in stock–recruitment analysis (Walters 1981; Walters and Lugwig 1981) and biased estimates of catchability (Shardlow and Hilborn 1985). Escapement counts are as important to salmon management as they are to fisheries theory. The majority of Pacific salmon stocks are managed on the basis of escapement targets, which are ideally determined by analysis of stock–recruitment relationships.

A literature review of previous studies of enumeration methods for escapement estimation was compiled by Cousens et al. (1982). This review found only one study (Brett 1952) that evaluated methods against a known number of fish. In Brett's study, a walking survey underestimated the Babine River fence count by two thirds. More recently, Solazzi (1984) compared numbers of coho, (*O. kisutch*), chinook (*O. tshawytscha*), and chum (*O. keta*) seen during foot surveys of an Oregon stream with the actual numbers present. Other studies have looked at variation between observer estimates (Sheridan 1962) for walking surveys. Enumerations by rafting and swimming are poorly documented, and no estimates of accuracy or precision of these techniques have been reported.

The purpose of this study was to (1) develop a quantitative framework for the relationship between how many salmon are seen in a river and how many are there, (2) compare the field counts made by different observers using several methods to the number of salmon known to be in the river, and (3) provide an estimate of the reliability of historical escapement data.

Components of Escapement Count

We propose a simple general model of fish behaviour and examine how the components of this model can be analyzed to determine the best estimate of escapement and confidence limits on the estimate, and to optimize the allocation of the escapement measurement effort. We are concerned only with the structure of the model and experimental analysis of some of the components. The analysis of confidence limits and optimum estimators will be developed in a separate study.

Assume that the arrival timing of the stock into the spawning area of the stream can be described by a vector q where q_t is the proportion of the total run that arrives in the spawning area on the tth day after the initiation of the run. If T is the total run size and r is the average number of days a fish is in the spawning area before it dies, then the number of fish present on any day t ($\hat{F}_t$) would be

$$(1) \quad \hat{F}_t = \sum_{i=(t-r+1)}^{t} (q_i T), \text{ where } t \geq r$$

$$\hat{F}_t = \sum_{i=1}^{t} (q_i T), \text{ where } t < r.$$

If we had daily estimates of the number of fish in the stream ($\hat{F}_t$), then

$$(2) \quad \hat{T} = \sum F_t.$$

In few, if any, cases will we have daily estimates of the number of fish in the streams; generally, streams are visited weekly, or even less frequently. We would need to determine a distribution for the $\hat{F}_t$'s and then estimate the missing days. This is often done by direct linear interpolation. There is a great potential to use Bayesian estimation using previous years' data on run timing for this type of estimation, but this will be the subject of later work.

It is impossible to see every fish in a stream. Therefore, the number of fish estimated to be in the stream at a specific time ($\hat{F}_t$) is the number actually seen divided by some estimate of the proportion seen. The proportion seen is generally accepted to depend on the species, time of the spawning cycle, physical stream characteristics, and weather conditions.

The relationship between the number of fish in a river on a given day and the number seen by a specific observer is the major subject of the experimental portion of this paper.

First, we examine the components of this relationship. The simplest relationship between the number seen (S) and the number in the river (F) is

$$(3) \quad S = pF$$

where p is the probability of any fish being seen; p will obviously depend on species, type of stream, observation method, and observers experience and is, in practice, left to individual field staff to estimate by their own methods. Depending on species and method, fish are easier to observe in some types of stream habitats than others. It is recognized, for instance, that during foot surveys, coho holding in pools are difficult to see, but are easier to see when they are on the spawning riffles.

We can extend equation (3) to allow for habitat diversity as

$$(4) \quad S_t = \sum_{i=1}^{n} p_i F_i$$

and therefore

$$(5) \quad F_t = \sum_{i=1}^{n} \frac{1}{P_i} S_i$$

where S_t is the total number of fish seen on the tth day, P_i is the probability of seeing a fish in the ith habitat, F_i is the number of fish in the ith habitat, n is the number of habitat types, and F_t is the total number of fish actually in the stream on the tth day.

If we believe that some methods of observation (walk, swim, raft) have different probabilities of seeing fish in each habitat, and that observer experience also affects the probability, then within a habitat and for a species

$$(6) \quad S_i = F_i P_m P_e$$

where P_m is the probability of a standardized observer seeing a fish with methods m and P_e is the proportional reduction in probability of detection by an observer of experience level e. There is the possibility of interaction between method and experience which is not considered in this paper.

Methods

The Big Qualicum River is a flow-controlled stream located on the east coast of Vancouver Island 60 km north of Nanaimo. The system has been the site of intensive biological activity since 1959. Fraser et al. (1983) described the system and reported on much of the investigation occurring prior to 1972. The 11-km river is fed through a control works at Horne Lake and drops rapidly over a series of waterfalls impassable to salmonids. The remaining 9 km of river, which constitutes the study area, winds its way through a partially logged valley and past a counting fence before entering the Strait of Georgia. The sole tributary, Hunt's Creek, is diverted through a flood channel to enter the Big Qualicum estuary. The vegetation adjacent to the river is dominated by alder trees, which form an exten-

sive canopy. Ninebark, red osier dogwood, and salmon-berry bushes form a moderately thick shrubbery along much of the stream margin. The river bed is approximately 20 m wide, with a slope of approximately 0.6% (Fraser et al. 1983). Flows ranged from 2.1 to 12.3 $m^3 \cdot s^{-1}$ during the course of this study.

The entire river was surveyed in the early 1960's (Anonymous 1962), and the survey marks established at that time were used to define sections of the river. There are 154 of these sections between the counting fence and the falls. In addition, 36 pools were defined for this study. These pools and sections formed the sampling units during data collection.

All five species of Pacific salmon inhabit the Big Qualicum River; however, only chinook, coho, and chum are present in appreciable numbers. Chinook migrate into the river from August through October and spawn mainly during the month of October. Coho enter from September to November and spawn from November to January, with peak spawning during December. Chum arrive in fresh water from October to December and spawn within 2 wk of arrival. Peak spawning for chum salmon occurs in late November and early December.

Survey Methods

By walking, observers working in pairs recorded the number of salmon seen by section and species. Separate counts were made for pools. The observers were instructed to use their own techniques and judgements to locate and count fish. Most observers did not depart far from the trail, since it followed the stream bank closely. Observers averaged 6 h to cover 9 km of stream.

The Big Qualicum offers some challenge to navigation, but rafting is feasible under most conditions. The rafts used were 3-m inflatables. An oarsman guided the raft from the stern, while an observer counted fish from the front of the vessel. Counts of each species were recorded separately for the river sections and pools. The raft trip took approximately 3 h and required several portages over log jams. The observers in both the rafting and walking surveys used Polaroid glasses whenever they felt it improved their ability to see fish.

In swimming, two surveyors fitted with mask, snorkel, and a dry suit observed the fish, while two recorders followed in a raft. The swimmers attempted to stay abreast of each other and coordinate their observations to obtain maximum coverage. In some portions of the river, swimmers would add their counts from each side of the river. In other parts, when the swimmers were forced close together, an average count was given. The number of fish seen in pools was recorded separately from those seen in the rest of the river.

Continuous fence counts of adult salmon entering the Big Qualicum River have been made since 1959. During this study, Big Qualicum Hatchery staff enumerated salmon entering the river, either through the counting fence or through the hatchery holding ponds. At the counting fence, all fish passing upstream are forced to pass over a white flash board where counts, by species, are made from an overhead vantage point. Due to the controlled flow of the river, and the experience of personnel involved, these counts are regarded as highly accurate. The fish that pass through the hatchery holding system are enumerated individually during sorting.

After the fish have been enumerated, they may be removed by the sports fishery or by natural die-off. The estimate of the number of fish alive in the river was gained from the fence count, minus sport catch and natural deaths. Chinook angling was closed during this study, so only natural deaths were subtracted for the chinook population estimate. For the majority of estimates, only the fence count was used because die-off was not large during the bulk of the study period. When die-off did occur, the rate was estimated by using the life span in days observed for chinook held at the Big Qualicum Hatchery. This life span (estimated to be 30 d) was allotted to all chinook past the fence on a given day. Coho salmon showed no evidence of die-off, so only the sport catch was subtracted from the coho fence count. The sport catch, estimated through a creel survey, was a small proportion (5%) of the fish in the river.

TABLE 1. Number of fish seen by species and method for the Big Qualicum River, Vancouver Island, B.C.

Species and method	Julian date	Number seen			Number in River	Fence Counts
		Pool	Riffle	Total		
Chinook, walk	255	51	0	51	185	185
	255	62	0	62	185	185
	265	25	8	33	339	339
	276	28	46	74	990	990
	290	129	535	664	2538	2877
Chinook, raft	256	44	45	89	294	294
	264	45	8	53	339	339
	270	49	8	57	612	612
	278	297	70	367	967	990
	291	354	623	977	2538	2877
Chinook, swim	257	150	110	260	310	310
	266	108	17	125	339	339
	271	176	15	191	990	990
	277	308	50	358	977	990
	292	806	648	1454	2539	2878
	295	236	422	658	2543	2882
	299	516	422	938	1897	2887
Coho, swim	257	0	0	0	1	1
	266	0	0	0	1	1
	271	0	0	0	59	59
	277	0	0	0	59	59
	292	2536	290	2826	4228	4336
	295	959	730	1689	4513	4657
	299	1308	335	1643	4765	4957
	306	2379	249	2628	5692	5968
	313	2134	828	2962	8511	8871

Results

River Experiment

Observations obtained from the different methods were compared to estimate the proportion of the population seen by each method (Table 1). The number of fish seen (S) for each method will be some proportion (p) of the population (F) present:

$$S = pF$$

and

$$(7) \quad F = \frac{1}{p} S.$$

Figure 1 shows the regression of the number of chinook in the river (F) against the number of chinook seen (S), in both

TABLE 2. Regression analyses of number of salmon in river against the number seen by method (*significant at the 0.05 level; **significant at the 0.01 level).

			Unconstrained regression			Constrained regression		
Method	Species	Trials (n)	$\frac{1}{p}$	p	r^2	$\frac{1}{p}$	p	r^2
Walk	Chinook	6	3.6**	0.28	0.91	3.94	0.25	0.88
Raft	Chinook	5	2.3**	0.43	0.97	2.64	0.38	0.93
Swim	Chinook	7	1.58*	0.63	0.63	2.12	0.47	0.62
Swim	Coho	9	2.25**	0.44	0.88	2.31	0.43	0.88

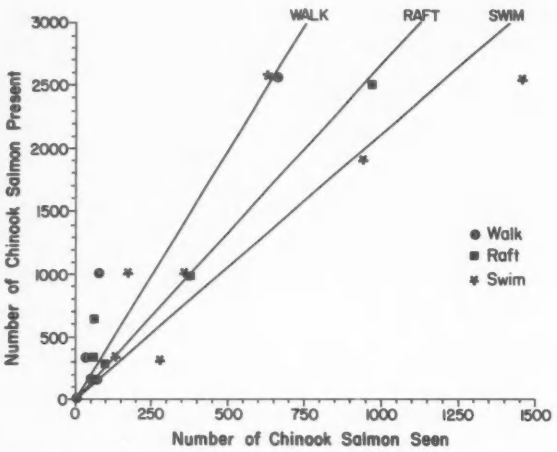

FIG. 1. Regression of chinook spawner population size versus number of spawners seen by each method.

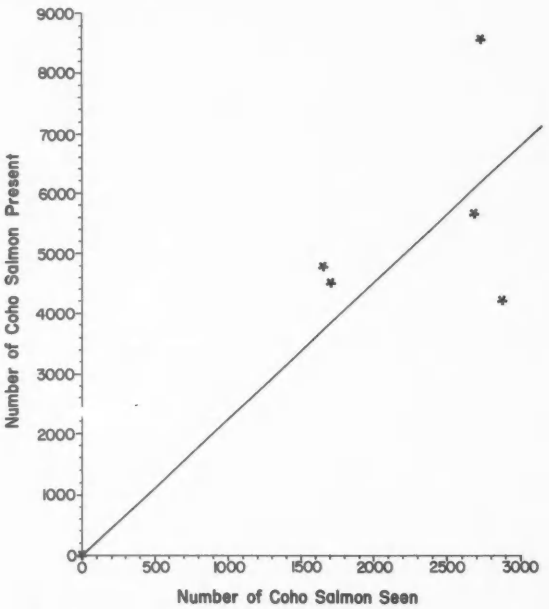

FIG. 2. Regression of coho spawner population size versus number of spawners seen by swimming.

pools and riffles, by each method. The probability of seeing a chinook (p) increased from walking (0.28) to rafting (0.43) to swimming (0.63) (Table 2). The regressions for each of these methods are significant beyond $\alpha = 0.05$, and from the coefficients of determination, we believe that the proportion seen by these methods is consistent (see r^2 in Table 2). Because the intercepts for these regressions were not significantly different from zero, the regressions were repeated and constrained through the origin. This analysis resulted in lower probability (p) for each method (Table 2).

Data for the coho salmon were only available for the swimming method (Fig. 2; Table 2). The coefficient of determination ($r^2 = 0.88$) was also high, but was largely determined by the single point at the origin. There is considerable variability in these data. However, these data suggest that the probability of seeing coho while swimming (0.44) is less than the probability of seeing chinook using the swimming technique.

Thus far we have not separated observations for habitat types. Pools and riffles were analyzed as separate habitats (Table 3) with an application of equation (6), i.e.

$$(8) \quad F_T = \frac{1}{p(\text{pools})} S + \frac{1}{p(\text{riffles})} S.$$

The probability of seeing a chinook in pools increased from walking to rafting to swimming. This was a function of the observer's increased ability to see into the pools. In shaded pools, newly arrived chinook and coho were difficult to see from the bank while walking. The colouring and hiding tendency made these fish almost invisible. However, they became more visible to observers in rafts or with face masks. For example, probability of seeing a chinook while walking was 0.18, rafting 0.33, and swimming 0.94 (Table 3).

TABLE 3. Probability of seeing salmon in pools and riffles by method as determined by a regression of number seen = probability of seeing a fish × number there.

		Probability		
Species	Method	Pool	Riffle	r^2
Chinook	Walk	0.18	0.29	0.93
Chinook	Raft	0.33	0.43	0.97
Chinook	Swim	0.94	0.29	0.90
Coho	Swim	0.64	0.19	0.97

In riffle habitat, however, seeing fish while swimming was more difficult than when using other methods. There was only a 29% chance of observing a fish when swimming in a riffle.

The chances were 29 and 43% by walking and rafting, respectively. One explanation for this is that riffles were shallow and the volume of water seen by a swimmer was less in a riffle than in a pool. In addition, salmon used pools as hiding refuges from predators. Thus, swimmers tended to scare the fish ahead of them into pools and out of riffles. In rafting, a compromise between walking and swimming was reached, in that an observer could see a larger volume of water in a riffle than when swimming due to his elevated position above the stream, but could not see into pools as well as when swimming. Therefore, the probability of seeing a chinook while rafting was 0.43 in the riffle and only 0.33 in pools.

Channel Experiment

The Big Qualicum River has a spawning channel designed for about 20 000 chum salmon. The channel's water source is the Qualicum River. The water passes over 11 950 m^2 of prepared spawning gravel forming a channel 1036 m long and 12 m wide with depths ranging from 45 to 60 cm. The channel, for the purposes of this study, represented a spawning riffle which contained a known number of fish. This spawning riffle, although not a natural stream riffle, was taken to represent counting under the most ideal circumstances of fish visibility within natural streams.

Observers used four methods of enumeration: overflight counts using fixed-wing aircraft and helicopter, walking counts that included streamside walks of the channel, and stationary counting of designated strips. The observers chosen for this study had a wide range of fish counting experience, from none at all to 15 yr of enumerating spawners.

Fixed-wing counts were obtained by flying over the channel at an altitude of 50 m and a speed of 90 knots in a Cessna 185. The observer recorded his estimate of fish in the channel as seen from the right window of the aircraft. Two passes were made over the channel for each observer. Helicopter counts also involved two passes over the channel. The pilot followed the instructions of each observer concerning position and altitude of the helicopter for counting. The altitude and time spent counting were the same for each trial (50 m and 10 min per observer).

After the fixed-wing and helicopter observations were made, the observers walked along the side of the channel and counted fish from the 1.5-m-high bank. Finally, six stations were set up within the channel and the number of fish within each station was counted by each observer. Each station, or strip, was 10 m long and 12 m wide. The strips were placed systematically through the channel.

Table 4 presents the summary of results from eight observers using the four different methods. Analyses were performed on two data sets, one which included all observers, regardless of experience, and another ("adjusted") which removed the data of the two least experienced observers (who had never estimated numbers of fish before). For the adjusted data, the mean percent of spawners estimated was closest to the actual population when counting was conducted from a helicopter (100.4%) and when walking (93.0%). Population estimates from fixed-wing aircraft and from strip counting were 84.9 and 84.0%, respectively. The coefficient of variation (C.V.) which is related to the percent estimated was highest for helicopter counts (0.24) and fixed-wing counts (0.21) and lowest for walking (0.10) and the strip method (0.073). If the inexperienced observers were included in the analysis, the mean percentages were drastic overestimates of spawner numbers, particularly for aerial counts, and the C.V.'s were higher than for the adjusted data. This discrepancy was not true, however, for the strip estimates, where neither the percent estimated nor the C.V.'s differed between experienced and inexperienced observers.

TABLE 4. Percent of chum spawners seen and coefficient of variation for four methods of counting salmon on a spawning riffle (adjusted data have had totally inexperienced observers excluded).

Method	Average	C.V.	Adjusted %	Adjusted C.V.
Helicopter	286.0	0.74	100.4	0.24
Fixed Wing	252.2	0.79	84.9	0.21
Walking	99.9	0.20	93.0	0.10
Strip estimate	87.0	0.067	84.0	0.073

Strip Estimation

Estimating spawner populations using strip counts involved summing the counts for the six strips and multiplying by the ratio of total area of the spawning channel to the area enumerated in the strips by each observer (total channel estimate, Table 5). The average percent of spawners estimated by the seven observers, as discussed earlier, was 87%.

An analysis of variance (Table 5) indicated that there were differences in counts among strips and among observers. That is, some individual observers were generally low, while others tended to be high. The influence of past experience at counting spawners showed no effect in influencing accuracy of counts by this method of enumeration. For example, observers 7 and 8, with the least experience, were as accurate as observers 1 and 6 in their estimate of the true population. This was not true for the other estimates of the channel population. While walking, for example, observers 7 and 8 estimated 50 000 and 7800, respectively, when the true population was 24 000.

Pool Experiments

The regression model described earlier provides us with an estimate of the probability of observing an individual fish present in a pool or a riffle. In an attempt to directly measure visibility of fish in a pool, we placed a small-mesh seine net around a major back eddy, completely sealing off this pool. Nine observers were then permitted several minutes to independently count the number of fish present from the stream bank. Each observer was then rowed around the pool once in a raft, and each observer was then given 5 min to swim in the pool. The fish in the pool were then seined with another net and enumerated. Table 6 shows the results of the experiment.

All methods underestimate the number of fish in the pool, with walking seeing the smallest proportion (4.4%), rafting a larger proportion (14%), and swimming the largest proportion (34%). Observers were classified by their experience level: two observers were highly experienced with over 10 yr of field counting of salmon, four observers were moderately experience in counting fish. We can analyze the effect of method and experience by the following model:

$$(9) \quad \text{(number seen)} = \text{(number there)}\ p_m p_e p_{me}$$

where p_m is the probability of an experienced observer seeing a fish with method m and p_e is the proportional reduction for experience level ($p_e = 1$ for experienced observers). Equa-

TABLE 5. Number of chum salmon seen by eight observers in six different sample strips of the Qualicum spawning channel.

Observer	Strip 1	2	3	4	5	6	Total no. counted	Total channel estimate	% of actual no. counted	Walk estimate
2	163	180	154	149	166	136	948	17 547	73	18 500
1	220	270	200	250	175	150	1265	23 415	98	27 200
3	148	154	145	132	149	150	878	16 242	68	22 100
6	191	215	162	142	165	166	1041	19 269	80	15 200
4	175	250	275	250	175	196	1321	24 452	102	29 000
7	200	300	225	175	250	170	1320	24 433	102	50 000
8	215	225	175	95	175	165	1080	19 991	83	7 800
Average	187	232	191	170	179	162		20 766	87	

TABLE 6. Number of coho salmon seen in a pool by different observers (365 were present during the experiment).

Observer	Walk	Raft	Swim	Experience level
A	8	50	250	High
B	11	150	150	High
C	3	23	180	Medium
D	2	12	50	Low
E	40	50	140	Medium
F	3	24	35	Low
G	44	85	120	Medium
H	3	1	70	Low
I	30	70	115	Medium
Average	16.0	51.7	123.3	

tion (9) can be transformed into equation (10) for ANOVA purposes:

$$(10)\quad \ln \frac{\text{number seen}}{\text{number there}} = \ln (p_m) + \ln (p_e) + \ln (p_m \times p_e).$$

The term $\ln (p_m \times p_e)$ is an interaction term. Equation (10) implicitly assumes that the errors are lognormal rather than the normal distribution assumed in our earlier regressions. We do not have sufficient data to test the shape of the distribution in a meaningful way, but we found that the multiplicative form of equation (10) had no significant interaction whereas an additive form had a significant interaction term. We therefore present the multiplicative model. There is no significant interaction, but both method and observer are highly significant. Table 7 shows the cells estimated from the analysis.

TABLE 7. Probability of a fish being seen in pools by different methods with different levels of experience.

Experience	Method Walk	Raft	Swim
High	0.04	0.15	0.53
Medium	0.04	0.14	0.51
Low	0.01	0.03	0.10

Discussion

The component model has served as a useful framework for the design and analysis of the experimental portions of this work. The model is so general and, in principle, so flexible that it could fit almost any type of spawning behaviour. It provides a basis for development of theory of escapement counting and refinement of current practice.

The experimental results have confirmed that species, habitat type, method of observation, and observer's experience all affect the probability of observing a fish. The results have generally conformed to prior expectations; chinook are easier to see than coho, fish are more visible in riffles than pools, fish in pools are more easily seen while observers are swimming than while walking, and experienced observers see a higher proportion of fish than inexperienced observers. However, there were some surprising results, the most surprising being the low proportion of fish that was seen by all methods. Although an increase in fish counted was expected when swimming, most participants were greatly surprised to swim the river and see hundreds or thousands of fish when they had only seen dozens previously while walking.

While we found that experienced observers observed a higher proportion of the fish than did inexperienced observers, the significant difference seems to be between totally inexperienced and those with some experience. Thus, it appears that modest amounts of training and experience should be sufficient to reduce the experience effect greatly. We also found that more standardized methods such as strip counting reduced the variability due to experience, and in locations where observers change frequently, it would be advizable to use standardized counting locations, rather than relying on total estimates.

While some methods see a higher proportion of fish than others, the methods also differ in their reliability as an index. The coefficients of determinations are similar for the two principal methods (walk, raft), but somewhat lower for swimming. The choice of method between walk and raft should be governed by ease of coverage, rather than intrinsic reliability. Therefore, although swimming does provide the highest proportion seen, the time, difficulty, and hazard entailed and the lower precision may make rafting and walking preferable because a raft or walk count appears to be as good an index of fish density as a swim.

These experimental results point to a number of obvious improvements in the data collection system. Data should be recorded by number observed in pools and numbers in riffles, as well as an estimate of the percent of pool area examined and

the percent of riffle areas. This would allow the number seen to be divided by the probability of being detected, thus providing an estimate of the number of fish actually in the stream.

In many rivers, difficulty of access or time limitation may make the use of standardized strips preferable to other methods. Since strips should occur primarily in spawning riffles, frequent visits would be necessary to make sure that the peak of the run is counted on the strips. The time saving of strip counting is substantial: it took 5–8 h to walk the Big Qualicum, while all the strips could be counted in an hour or two; thus, the optimal allocation of field time may mean many strip counts rather than few walks, rafts, or swims.

A major purpose of this paper was to evaluate the reliability of historic escapement data that have been used in scientific papers and for management. We have found that in all cases, only a fraction of the salmon in the river were seen by the methods used. Most estimates of total spawners involve expanding the number seen by some factor. These factors have not been standardized or documented. It was our experience that expansion factors for the large part are conservative and do not account for the smaller-than-expected proportion seen. Our major conclusion is that most British Columbia escapement data collected by walk, raft, swim, or aircraft are probably underestimates. Since there is no reason to suspect a change in the underestimation during the period of the current escapement data (1952 to the present), the estimates of harvest rates are undoubtedly high, as are our estimates of allowable harvest rates.

It is more difficult to determine the variability of the estimates. This is the "observation error" of Walters (1981). The C.V.'s we derived for the different methods are a minimum estimate because the variability of the estimated number of fish spawning depends on the variances of three factors: the variance of the estimates of the number of fish in the stream at a specific time, the variance of the methods used to calculate the number of fish days present, and the variance of the instream residence time. As more information is acquired on the other two factors, we will start to understand the total magnitude of past estimates.

Finally, it is clear that a great deal of further research is needed on escapement methods. Similar experiments, when known numbers of fish are counted by different methods, need to be performed on other streams with different attributes. We would expect that visibility would be greatly affected by stream size and flows, but this needs to be tested. The length of stream residence needs to be measured for different species in different locations; it needs to be determined if stream residency periods change from year to year and within the year. Most importantly, it needs to be recognized that escapement counting is a scientific problem that deserves to be treated as such, with experiments performed and standardized methods developed.

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Short-Term Effects of Zooplankton Manipulations on Phosphate Uptake

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Hamilton, D. T., and W. D. Taylor. 1987. Short-term effects of zooplankton manipulations on phosphate uptake. Can. J. Fish. Aquat. Sci. 44: 1038–1044.

Samples of epilimnetic water were collected, manipulated to alter their zooplankton fauna, and incubated in situ for 24 h. We hypothesized that removal and concentration of zooplankton would decrease and increase phosphate turnover time, respectively, and that the presence of zooplankton would increase the accumulation of added $^{32}PO_4$ by algae (particles greater than 1.0 μm) relative to bacteria (particles 0.2–1.0 μm). Although the treatments produced significant changes in turnover time and size distribution, neither hypothesis was supported; removal of zooplankton did not decrease turnover time, and it reduced the dominance of 0.2- to 1.0-μm particles in phosphorus uptake. However, concentrating microzooplankton frequently increased turnover time. Zooplankton removal caused a relative increase in ciliates, suggesting that these protozoa may be limited by their predators rather than by resource levels. Our results suggest that microzooplankton were the most important grazers and that the nutrient environment of phytoplankton was not directly affected by mesozooplankton. Phosphate dynamics were probably determined by bacteria, the protozoan predators of bacteria, and the supply of dissolved organic carbon.

Des échantillons d'eau ont été recueillis dans l'épilimnion, manipulés afin de modifier leur faune zooplanctonique puis incubés *in situ* pendant 24 h. Les auteurs formulent les hypothèses que l'enlèvement et la concentration du zooplancton abaisse et augmente respectivement le temps de renouvellement du phosphate et que la présence du zooplancton stimule l'accumulation du $^{32}PO_4$ ajouté chez les algues (particules plus grosses que 1,0 μm) par rapport aux bactéries (taille des particules de 0,2 à 1,0 μm). Quoique les traitements aient produit des modifications importantes du temps de renouvellement et de la répartition des tailles, aucune des hypothèses n'a été étayée; l'enlèvement du zooplancton n'a pas abaissé le temps de renouvellement quoiqu'il ait réduit la dominance des particules de 0,2 à 1,0 μm pour ce qui est de la captation du phosphore. Toutefois, la concentration du microzooplancton a fréquemment augmenté le temps de renouvellement. L'enlèvement du zooplancton a amené une augmentation relative des ciliés, ce qui porte à croire que ces protozoaires peuvent être limités par leurs prédateurs et non par les niveaux de ressources. Les résultats portent à croire que le microzooplancton est le plus important brouteur et que l'environnement nutritif du phytoplancton n'est pas directement touché par le mésozooplancton. La dynamique du phosphate est probablement déterminée par les bactéries, les prédateurs protozoaires des bactéries et l'approvisionnement en carbone organique dissous.

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Primary production may continue in stratified, nutrient-depleted surface waters without significant inputs of nutrients from external sources. Remineralization of nutrients by heterotrophic organisms is believed to supply the needs of autotrophs. Heterotrophic bacteria may release phosphates in breaking down organic matter, but since they depend largely on organic carbon released by living algae in planktonic systems (Sondergaard et al. 1985), they are probably important competitors of algae for phosphate and ammonium in planktonic ecosystems (Rigler 1956; Rhee 1972; Mayfield and Inniss 1978; Currie and Kalff 1984b). Therefore, holozoic organisms, which consume other organisms and therefore should mineralize nutrient elements at least in proportion to the carbon they oxidize in respiration, should be the major source of nutrients. The relative rates of phosphorus release by large and small zooplankton have been suggested as part of the mechanism that changes phytoplankton biomass in response to changes in zooplankton size distribution (e.g. Lehman 1980; Bartell 1981; Stenson 1982).

Demonstrating the role of zooplankton in supplying the phosphorus demands of bacteria and algae has been difficult. Although zooplankton release of phosphate may account for much of the observed primary production (Lehman 1980; Korstad 1983), the actual flow of phosphate is primarily into bacteria-sized particles (Taylor and Lean 1981; Lean and White 1983; Currie and Kalff 1984b), and the release of phosphorus from zooplankton is small compared with the total flux from the dissolved phase to the particulate phase in lakes (Taylor 1984, and unpublished) and in bacterial cultures (Taylor 1986). This discrepancy may be because the phosphate uptake measured with radiotracers is a gross uptake and very much larger than net uptake (Lean and Nalewajko 1976; Lehman 1984). But there is nothing to suggest that net uptake is partitioned selectively into algae. In an oligotrophic marine environment, Smith et al. (1985) found that phosphorus flux into particles was not in excess of independent estimates of

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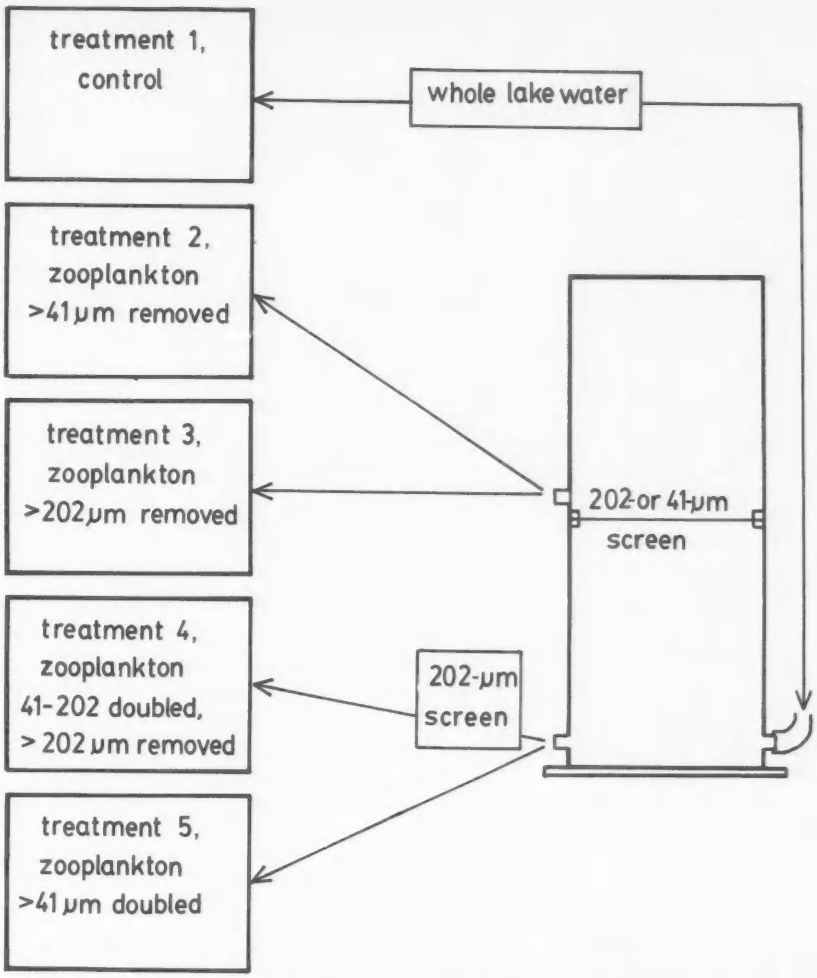

FIG. 1. Diagrammatic representation of the apparatus used to manipulate zooplankton populations, and a flow chart to describe the preparation of the five treatments.

plankton growth. That net phosphate uptake is not greatly less than gross uptake is also suggested for freshwater by the observation that addition of PO_4 cannot displace labelled phosphorus from the particulate phase (Grillo and Gibson 1979; Brown and Button 1979). Our inability to resolve these questions results from our inability to measure PO_4 at low ambient concentrations.

Despite uncertainty about whether the gross uptake of phosphate measured by radiotracers is much greater than the net flux into bacteria and algae, we can accept that the phosphate turnover time measured with radiotracers is an index of supply relative to demand. Zooplankton should increase the supply/demand relationship by nutrient release (increasing supply) or by grazing (reducing demand). Therefore, manipulation of zooplankton communities should produce changes in phosphorus turnover time. Because increasing the phosphate concentration shifts the size distribution of $^{32}PO_4$ taken up toward larger cells (Taylor and Lean 1981; Lean and White 1983), zooplankton excretion should also favour radiotracer uptake by large cells. This should be especially true if large zooplankton create nutrient patches (Lehman and Scavia 1982).

The purpose of this work was to test the hypothesis that zooplankton greater than 40 µm (larger microzooplankton and mesozooplankton) play a significant role in determining the nutrient environment for algae and bacteria, and if so, to determine the relative importance of microzooplankton and mesozooplankton. We proceeded by removing or concentrating zooplankton and measuring the effects on phosphate turnover time and the size distribution of assimilated phosphorus.

Materials and Methods

Our study site was the deepest point (43 m, in Sharpes Bay) of Jacks Lake in southern Ontario (78°03′W, 44°44′N). This bay is mesotrophic (total phosphorus = 12 $\mu g \cdot L^{-1}$, chlorophyll = 4 $\mu g \cdot L^{-1}$). Relevant studies at this site include

Taylor and Lean (1981), Lean and Pick (1981), and Lean and White (1983). Main experiments were conducted beginning June 2, July 29, and August 24, 1983.

Water was taken at a depth of 5 m using a Van Dorn sampler, placed in two 20-L opaque polyethylene jugs, and brought to a shore laboratory. Samples were fixed for phytoplankton and zooplankton enumeration. Five treatments were performed using a cylindrical Plexiglas tower with a removable nylon screen dividing it into two 2-L chambers (Fig. 1). The tower was filled from the bottom so that organisms would be excluded from the upper chamber and concentrated in the lower chamber. Both chambers had drain ports. Four 1-L polyethylene bottles were filled for each treatment: two for measurement of phosphate turnover time and two for the measurement of ^{32}P size distribution. The latter were spiked immediately with approximately 50 kBq of carrier-free $^{32}PO_4$, and all 20 bottles were returned to the lake for in situ incubation at a depth of 3 m (which approximately compensates for the 37% reduction of light by the bottle). A floating rack was constructed that hung each bottle separately, so that they could be sampled without exposing others unnecessarily to surface light and to reduce shading of the bottles.

Measurements of phosphate turnover time were made at 8 and 24 h for both replicates of each treatment. Samples from each of the 10 bottles were returned to the laboratory, and 50-mL aliquots were spiked with about 16 kBq of carrier-free $^{32}PO_4$. Then, 1-mL aliquots were filtered at 1, 2, and 3 min (2 June) or 0.5, 1, and 2 min (July 29 and August 24) through 0.2-μm Nuclepore filters. Filters were placed in scintillation vials, as were 500-μL aliquots for the determination of total radioactivity. When the 24-h filtrations were completed, the remaining unlabelled water (about 800 mL) was poured through a 30-μm Nitex screen. The contents of the screen were fixed with 5% formalin for zooplankton counts, and the filtrate was fixed with 1% Lugol's iodine for determination of ciliates and phytoplankton.

Polycarbonate filters were dissolved in the scintillation vials with 100 μL of a 10% (v/v) solution of monoethanolamine in methylene chloride. Fluor was then added (7 mL PCS, Amersham for polyethylene minivials) and the vials were counted for 10 min or 10^5 disintegrations on a Searle model 6880 scintillation counter.

The amount of radioactivity retained on the filters was transformed to the natural logarithm of the percent of radioactivity remaining in solution. The exponential rate of decrease of ^{32}P in solution measures the uptake constant for phosphate, and the reciprocal of the slope is the phosphate turnover time. The point time = 0, percent in filtrate = ln (100%) was used as a data point for May 31 and July 29, but not for August 24 because it changed the slope; time = 0 uptake was slightly greater than 0.

The 8- and 24-h measurements were analyzed separately. The uptake constants were derived by least-squares regression and an analysis of variance was completed. If heterogeneity of the slopes was found, Student–Newman–Keuls multiple range test was used to determine homogeneous groups.

The size distribution of ^{32}P was determined after 2 and 24 h of incubation. From both replicates of each treatment, 30-mL samples were brought back to the shore laboratory, and 5-mL aliquots were filtered through each of 0.2-, 1.0-, and 12.0-μm Nuclepore filters. The filters were placed in scintillation vials, as were two 500-μL aliquots for the determination of the total radioactivity. Treatment and counting of the samples were as for the turnover time measurements. Activity retained on the filters was converted to a proportion of the total radioactivity, and then the proportion of ^{32}P less than 0.2, 0.2–1.0, 1.0–12.0, and greater than 12.0 μm was calculated.

TABLE 1. Metazoan zooplankton in the experimental bottles after 24 h. These counts represent 75% of the volume in the two replicates used for measuring turnover time.

Date	Taxon	Treatment 1	2	3	4	5
June 2	Rotifera	316	16	198	346	434
	Cladocera	6	0	2	2	2
	Cyclopoida	58	0	24	27	61
	Calanoida	0	0	0	0	10
	Nauplii	9	0	9	27	22
June 29	Rotifera	57	2	107	112	15
	Cladocera	9	0	0	1	11
	Cyclopoida	4	0	14	11	14
	Calanoida	5	0	2	6	13
	Nauplii	27	0	43	91	43
August 24	Rotifera	48	7	21	37	33
	Cladocera	9	0	1	0	2
	Cyclopoida	19	0	31	25	33
	Calanoida	1	0	1	0	5
	Nauplii	18	0	50	50	38

Prior to analysis, proportions were transformed as the logarithm of the odds ratio, log (Pi/1 − Pi), where Pi is the proportion of ^{32}P in the *i*th size-class (G. Bennet, University of Waterloo Statistical Consulting Service, pers. comm.). Homogeneity of variance was examined using Levene's test (Snedecor and Cochran 1980); in 3 of 12 cases (4 size-classes × 3 experiments) there were marginally significant departures from homogeneity. These should affect the analysis of variance only when there are marginally significant results for those size-classes. The proportions for each experiment were analyzed separately using one-way analysis of variance. Significant differences were isolated a posteriori with Duncan's multiple range test.

Phytoplankton and ciliates were counted in settling chambers with an inverted microscope. Cell volumes of phytoplankton were determined from linear dimensions and converted to biomass using a conversion factor of 1.0 $g \cdot mL^{-1}$.

Two ancillary experiments were conducted: one to examine the direct effect of the treatments on phytoplankton and one to contrast the fate of ^{32}P excreted by *Daphnia* with that added as carrier-free $^{32}PO_4$. For the treatment–effect experiment, a 2-L sample of lake water was spiked with $^{32}PO_4$ and incubated for 2 h. Then, 5-mL aliquots were filtered through 0.2-, 1.0-, and 12.0-μm Nuclepore filters before manipulation, after concentrating particles greater than 41 μm, as in treatment 5, and after removing particles greater than 41 μm, as in treatment 2.

For the excretion–fate experiment, $^{32}PO_4$-labelled lake water was incubated for 18–24 h in situ or in an incubator at the University of Waterloo. Labelled *Daphnia* were harvested and washed: four were placed in each of two vials containing 100 μg P (as $PO_4) \cdot L^{-1}$ in 0.2-μm-filtered lake water (no uptake of excreted material due to lack of organisms and competitive inhibitor); four were placed in each of two vials containing 25 mL of whole lake water; and four were placed in each of two vials with 25 mL of whole lake water, but which

TABLE 2. Phytoplankton biomass (μg wet weight·L^{-1}) and ciliate abundance (no.·mL^{-1}) in the experimental bottles before (T_0) and 24 h after treatment.

Date	Taxon	Treatment					
		T_0	1	2	3	4	5
June 2	Phytoplankton	230	720	479	660	660	1660
	Ciliates	15.2	9.5	13.3	15.5	11.9	10.7
July 29	Phytoplankton	931	870	400	620	940	750
	Ciliates	12.1	9.5	11.8	8.6	9.3	6.5
August 24	Phytoplankton	560	920	470	760	720	1100
	Ciliates	—	12.0	16.6	11.8	11.2	10.3

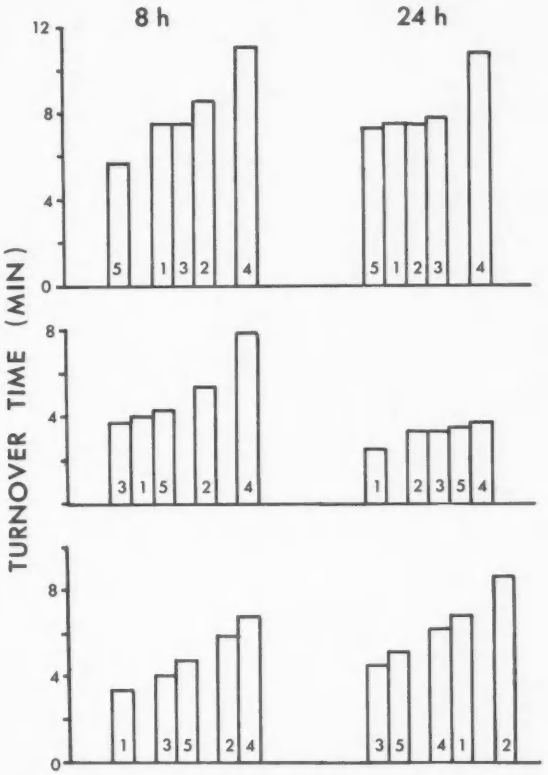

FIG. 2. Turnover times for phosphate at 8 and 24 h after the various treatments. Spaces between treatments indicate significant differences. The results for June 2, July 29, and August 24 are given from top to bottom.

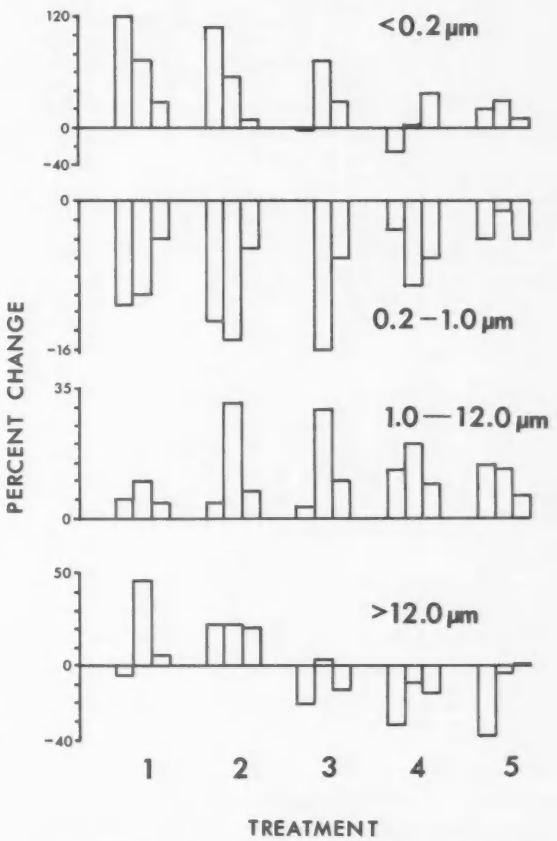

FIG. 3. Percent change in the proportion of ^{32}P in four size-classes of plankton between 2 and 24 h after treatments 1–5. For each treatment and size-class, the results for the three experiments (June 2, July 29, and August 24) are provided as three adjacent bars. Note that the scales vary.

were stirred by bubbling. The six vials were incubated for 20 min, the *Daphnia* were then removed, and the contents of the vials were filtered sequentially through 0.2-, 1.0-, and 12.0-μm Nuclepore filters to determine the size distribution of the excreted label, the size distribution of the label after uptake of available fractions by the plankton, and the size distribution of released label after uptake by the plankton with stirring to prevent patch formation (Lehman and Scavia 1982).

Results

The abundance of metazoan zooplankton was severely reduced by treatment 2 on all experimental dates; crustacean zooplankton were eliminated (Table 1). Treatment 3 left rotifers and copepods, but Cladocera were largely removed. Treatment 4 also had few Cladocera, but usually had more rotifers and nauplii than treatment 3. Treatment 5 had elevated copepod biomass, but rotifers and Cladocera were variably affected.

TABLE 3. Percentage of ^{32}P in four size-classes at 2 and 24 h after treatment for three experiments. Numbers in parentheses are ranks where there is significant heterogeneity of means ($P < 0.05$). Tied ranks indicate membership in homogeneous groups, and fractional ranks indicate membership in two groups.

Date	Elapsed time (h)	Size-class (μm)	Treatment 1	2	3	4	5
June 2	2	<0.2	5.6	6.6	7.8	6.0	6.3
		0.2–1.0	71.7 (4)	66.7 (2.5)	64.0 (1.5)	62.0 (1)	69.6 (3.5)
		1.0–12.0	21.5	25.8	26.8	29.7	17.3
		>12.0	1.2 (2)	0.8 (1)	1.3 (2)	2.4 (4)	1.9 (3)
	24	<0.2	12.2	13.8	7.7	4.5	12.2
		0.2–1.0	64.0	58.3	63.7	60.4	66.5
		1.0–12.0	22.6 (1)	26.9 (2)	27.5 (2)	33.6 (3)	24.3 (1.5)
		>12.0	1.2 (1)	1.0 (1)	1.1 (1)	1.6 (2)	1.1 (1)
July 29	2	<0.2	5.8	5.8	5.9	5.3	7.6
		0.2–1.0	71.0	70.5	69.2	70.1	68.3
		1.0–12.0	20.8	22.2	22.5	21.8	21.4
		>12.0	2.4 (2)	1.5 (1)	2.4 (2)	2.8 (3)	2.7 (2.5)
	24	<0.2	10.1	9.0	10.1	7.2	9.7
		0.2–1.0	63.5	60.1	58.4	64.0	63.4
		1.0–12.0	22.8 (1)	29.0 (3)	29.0 (3)	26.3 (2)	24.3 (1.5)
		>12.0	3.5 (2)	1.9 (1)	2.5 (1)	2.6 (1)	2.6 (1)
August 24	2	<0.2	5.9	6.9	7.0	5.4	5.4
		0.2–1.0	68.2 (2)	62.4 (1)	64.5 (1)	65.1 (1)	64.6 (1)
		1.0–12.0	23.2 (1)	28.7 (2)	25.8 (2)	26.4 (2)	26.6 (2)
		>12.0	2.8 (2.5)	2.0 (1)	2.8 (2)	3.2 (3.5)	3.4 (4)
	24	<0.2	7.5	7.5	8.8	7.4	6.0
		0.2–1.0	65.5 (2)	59.3 (1)	60.5 (1)	61.0 (1)	62.3 (1.5)
		1.0–12.0	24.1 (1)	30.7 (2)	28.3 (2)	28.8 (2)	28.3 (2)
		>12.0	3.0 (2)	2.4 (1)	2.4 (1)	2.8 (1.5)	3.4 (3)

The phytoplankton populations differed in treatments by 24 h after manipulation; treatment 2 generally had the lowest biomass, and treatments 4 and 5 had the highest (Table 2). *Chrysochromulina parva, Rhodomonas minuta, Katablepharis ovalis*, and *Chromulina* sp. were biomass dominants throughout the summer. *Cyclotella bodamica* was also important in July and August. Other important species in July were *Chlamydomonas sagittula* and *Oocystis parva*. In August, *Chroococcus limneticus* and *Gomphosphaera lacustris* were a significant proportion of phytoplankton biomass.

Ciliated protozoa were also affected by the manipulations (Table 2); their abundance was always highest in treatment 2 and lowest in treatment 5. The difference between treatments 2 and 5 was between 27% (2/6) and 56% (29/7) of control abundance.

The experimental manipulations produced significant differences among treatments in phosphate turnover time. Treatment 4 usually had the longest turnover time and was significantly longer than the control at 8 h after treatment on all experimental dates (Fig. 2). Treatment 2 also had a long turnover time in August and surpassed treatment 4 by 24 h. Treatment 5 had the shortest turnover time in June, when it also had the greatest number of rotifers and copepods. The control or treatment 3 had the shortest turnover times in the July and August experiments.

The treatments also produced significant changes in ^{32}P size distribution (Table 3). The most consistent effect that there was less ^{32}P in the >12-μm fraction for treatment 2. The treatment–effect experiment demonstrated that statistically significant changes of a similar magnitude could be generated in the >12-μm fraction directly by the screening manipulations, so experimental artifact likely contributes to this result. However, because this size-class also tended to increase its share of ^{32}P between 2 and 24 h (Fig. 3), indirect effects due to the zooplankton manipulations are also implicated.

The 1- to 12-μm fraction also differed significantly among treatments by 24 h after treatment on all dates (Table 3). The removal treatments (2 and 3) generally had more ^{32}P in this size-class, and this effect strengthened between 2 and 24 h (Fig. 3). The 0.2- to 1.0-μm fraction lost ^{32}P under all treatments, but most strongly in the removal treatments (2 and 3) and least in the concentration treatment (5). Although differences between treatments and changes between 2 and 24 h were often large for the <0.2-μm fraction, they were never statistically significant.

Turnover time and ^{32}P size distribution were not related in the expected fashion. For example, the >12-μm fraction lost ^{32}P between 2 and 24 h for treatments 4 and 5 in the June experiment (Fig.3), but these treatments had the longest and shortest turnover times, respectively (Fig. 2). The >12-μm fraction gained ^{32}P strongly in treatment 1 for the July experiment, but this treatment had the shortest turnover time at 8 h.

The fate of ^{32}P released by *Daphnia* into whole lake water was compared in stirred and unstirred containers. There was no effect of stirring on the size distribution of ^{32}P after assimilation by the particulate phase (Mann–Whitney test).

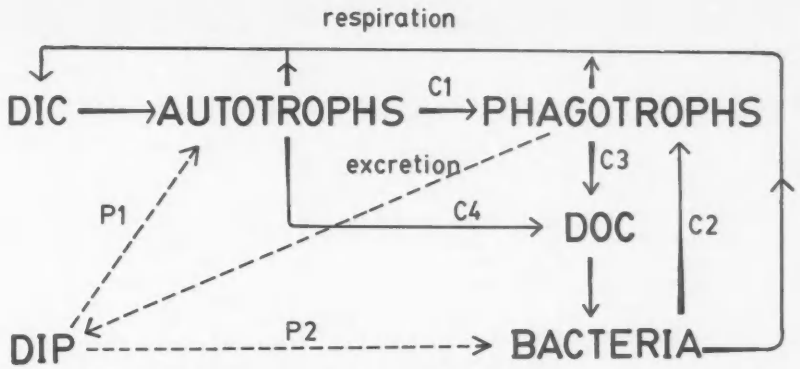

FIG. 4. Flow chart depicting the movement of carbon and phosphorus in a simplified plankton community. Broken lines indicate phosphorus movements. DIC and DIP indicate dissolved inorganic carbon and phosphorus, respectively.

Discussion

In none of our experiments did the removal of zooplankton >41 μm (treatment 2) cause the expected decrease in phosphate turnover time. In the August experiment, it caused a significant increase relative to the control. Removal of zooplankton >202 μm (treatment 3) seldom had pronounced effects, but in August it produced a shorter turnover time than the control, and a remarkably opposite effect to treatment 2. Treatment 5, the concentration of all zooplankton >41 μm should have increased turnover time, especially relative to treatment 2. It had the shortest turnover time in June, a turnover time longer than the control but not the other treatments in July, and a shorter turnover time than treatments 1 and 2 in August. Treatment 4, in which only zooplankton 41–200 μm were increased while zooplankton greater than 200 μm were removed, had a longer turnover time than treatment 5 in all cases. These results together suggest that nutrient excretion by metazoan zooplankton was not an important determinant of the phosphate environment for bacteria and phytoplankton.

The effects of zooplankton manipulations on ^{32}P size distribution are complicated by direct treatment effects, but changes between 2 and 24 h after treatment still can be used to determine changes in the pattern of phosphorus uptake. The 0.2- to 1.0-μm fraction appeared to lose ^{32}P between 2 and 24 h in all treatments, perhaps indicating attachment of bacteria to vessel walls. Alternatively, loss of ^{32}P from this size-class could be expected if the zooplankton density in the treatments, prepared in the morning when zooplankton are mostly deeper than 5 m, was generally low; zooplankton may have a positive effect on bacterial PO_4 uptake (see below). The loss from 0.2- to 1.0-μm particles was greatest in the June 2 and July 29 experiments, and contrary to our initial hypothesis, greatest for the removal treatments (2 and June 2 and 3 on July 29). The 1- to 12-μm fraction, which should mostly contain small autotrophs, was favoured by the two zooplankton concentration treatments (4 and 5) on June 2, but showed greater increases in the removal treatments (2 and 3) on July 29.

Our experiments indicated that ciliates (which are primarily 10–50 μm long in Jacks Lake, and therefore not directly manipulated during our experiments) are adversely affected by metazoan zooplankton, especially cyclopoids. Similar observations were made by Stenson (1984). The increase in ciliates which was produced may have masked the expected effects of the manipulations. The ability of ciliates to increase phosphate turnover time has been demonstrated in laboratory cultures (Taylor 1986). However, if this was true, we must accept that a 50% increase in ciliates overwhelms the effect of totally removing the metazoa. The relative importance of protozoa in grazing and nutrient regeneration can be substantial (e.g. Capriulo and Carpenter 1983; Taylor 1984; Verity 1985), and this explanation of our results, that protozoan zooplankton are much more important than metazoan zooplankton, cannot be excluded. Also, we did not enumerate the bactivorous microflagellates, and they may also have responded to our treatments. Although nonpigmented flagellates are not particularly numerous in Jacks Lake (F. R. Pick, York University, Downsview, Ont., pers. comm.), they may be the important predators of bacteria in pelagic systems (Fenchel 1982), and 0.2- to 1.0-μm particles clearly dominated phosphorus uptake during these experiments. Autotrophic flagellates are abundant in Jacks Lake, and some of these may be bactivorous (Bird and Kalff 1986).

A second, complimentary explanation is that competition between autotrophs and heterotrophs for phosphorus, and the overall phosphorus demand, is mediated by the supply of organic carbon (Brown et al. 1981; Currie and Kalff 1984a). Since algae are ultimately, if not directly, responsible for the supply of organic carbon, bacteria cannot eliminate them by competing successfully for phosphate, as they may in a laboratory system (Mayfield and Inniss 1978). If zooplankton are important to the carbon supply to bacteria, e.g. through excretion, egestion, or "sloppy feeding," then the anticipated effects of their removal would again be masked. A simple steady-state model of carbon and phosphorus flux can be constructed (Fig. 4) that illustrates this effect. The carbon fluxes C1 and C2, the predation on autotrophs and bacteria, respectively, must be accompanied by net phosphorus uptakes, P1 and P2. That bacterial PO_4 uptake (P2) apparently exceeds autotrophic PO_4 uptake (P1) may reflect that bactivory (C2), which at steady state is the dissolved organic carbon (DOC) production less bacterial respiration, is greater than the real growth of autotrophs. That zooplankton removal has positive or ambiguous effects on turnover time may indicate that C3, especially that component of it that can be directly affected with a 41-μm screen, is an important part of the DOC supply

to bacteria (Laird et al. 1986). Removal of large zooplankton could then decrease the supply of inorganic phosphorus, but reduce the phosphorus demand of bacteria.

At the low PO_4 levels found in Jacks Lake, dissolved organic phosphorus may be a significant source of phosphate for algae and bacteria. Because its origin from both algae (e.g. Lean and Nalewajko 1976) and zooplankton (e.g. Taylor and Lean 1981) and its fate (Currie et al. 1986) are probably only quantitatively different from PO_4, it can probably be included with dissolved inorganic phosphorus (DIP) in Fig. 4. However, its greater use by algae may help account for the apparent paradox that P2 is much greater than P1 (Currie et al. 1986).

The smaller microplankton and nanoplankton grazers are sometimes considered to be inefficient (e.g. Nilssen 1978; Shapiro and Wright 1984), but the meaning of inefficient is vague in this context. Assimilation efficiency is known to be higher in unicells than metazoa, not lower (Calow 1977; and see Goldman et al. 1985 for a discussion of relevance to this problem), and numerical response thresholds are thought to be higher in smaller protozoa than larger ones (Fenchel 1982). The idea of lower efficiency in protozoa relative to metazoa may be an extension of the concept that small animals are generally inferior competitors compared with large ones, but this is also poorly supported (Hall et al. 1976; Persson 1985). These experiments suggest that ciliates increase quickly in response to the removal of their predators, indicating that they may not be food limited. They may be capable of further decreasing their food resources, and alleviating nutrient limitation, when their predators are reduced.

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Modeling and Forecasting Primary Production Rates Using Box–Jenkins Transfer Function Models

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Box–Jenkins transfer function models were developed for time series of integrated hourly primary production rates. A 28-mo record of 56 biweekly measurements collected from seven mesocosms during a nutrient addition experiment was analyzed. Incorporation of two input variables (phytoplankton biomass and hourly light) significantly improved the fit of the models. When compared with standard regression models, the time series models all had reduced residual variance. The forecasting ability of the final fitted model for a control system was demonstrated with independent data from the two replicate control mesocosms.

On a élaboré des modèles Box–Jenkins à fonction de transfert pour des séries temporelles de taux horaires intégrés de production primaire. Cinquante-six données bimensuelles recueillies pendant 28 mo dans sept mésocosmes qui ont fait l'objet d'apports nutritifs expérimentaux ont été analysées. L'inclusion de deux variables (biomasse phytoplanctonique et luminosité horaire) ont grandement amélioré l'ajustement des modèles. Comparés aux modèles normalisés de régression, les modèles basés sur ces séries temporelles avaient tous une plus faible variance résiduelle. La capacité de prévision du dernier modèle ajusté pour un système témoin a été démontrée avec des données indépendantes recueillies dans deux mésocosmes témoins.

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In the analysis of primary production data, one is often confronted by simultaneous time series of integral productivity and various environmental factors, observed at some constant interval. Attempts to separate and quantify the effects of the various factors (chemical, physical, biological), which together control phytoplankton production, have frequently relied on correlation and regression analyses (Margalef 1965; Goldman et al. 1968; Platt and Subba Rao 1970; Hameedi 1976; Cote and Platt 1983, 1984). Generally, such efforts have revealed that productivity in estuarine systems is, most simply, a function of phytoplankton biomass and light availability (Gieskes and Kraay 1977; Falkowski 1981; Boynton et al. 1982; Cole and Cloern 1984). Predicting the productivity of the phytoplankton in nutrient-rich waters has centered around simple regression models based on these two factors. However, questions concerning the dynamics of a series of production measurements may not be answered by means of regression analysis alone. For example, is it possible to predict the future productivity of a system based on its past behavior? Does the dynamic behavior of production rely more on light history or more on prior values of biomass?

Characterizing dynamic systems may be undertaken in a variety of ways. One method, time series analysis (Box and Jenkins 1976), has been a successfully applied predictive technique in diverse fields (Poole 1972, 1976; Boudreault et al. 1977; Saila et al. 1979; Mendelssohn 1981; Kato 1985). In this paper, the use of transfer function models (Box and Jenkins 1976) for modeling and forecasting phytoplankton production dynamics is explored. Transfer function models (single output–multiple input) are a subclass of the Box–Jenkins ARIMA (autoregressive-integrated-moving-average) models, a group of linear, stochastic models that can describe fairly complex behavior. Univariate ARIMA models represent a response time series (Y_t) as a linear combination of its own past values (i.e. an autoregressive component) and current and past values of the error term (i.e. a moving average component). Transfer function models incorporate not only the past history of the output variable (Y_t) but also the current and past history of other related input variables ($X_{1t}, X_{2t}, \ldots, X_{it}$). Application of transfer function models is demonstrated on a 28-mo record of 56 biweekly values for hourly ^{14}C production and its associated input variables, phytoplankton biomass, and incident light. Forecasts of the dependent variable, production, are based on its own history and its relation to the two independent variables, biomass and light.

The data were collected from nine large-scale mesocosms (for a description, see Oviatt et al. 1986a) employed in a nutrient addition experiment at the Marine Ecosystem Research Laboratory (MERL) at the University of Rhode Island. Nine data sets, comprising three control and six experimental systems (with nutrient inputs of 1, 2, 4, 8, 16, and 32 times the average annual loading of the natural system, Narragansett Bay), were available for analysis. The specific purpose of this paper was to develop and compare transfer function models based on two input variables, biomass and light, for a control system and the six experimental systems. Many factors other than biomass and light affect photosynthesis, most notably nutrient availability. Preliminary analyses indicated that incorporation of nutrient loading levels did not significantly improve the models. Oviatt et al. (1986a) demonstrated a linear relationship between water column production and nutrient loading for the seven experimental treatments, suggesting that primary production did not reach a saturation limit. Mean chlorophyll *a* values over the experimental period

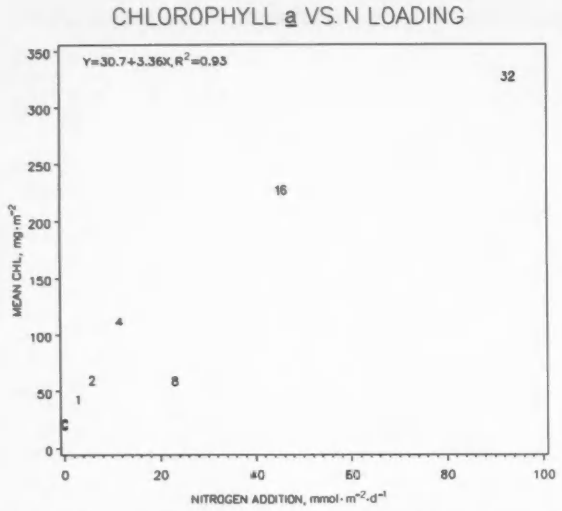

FIG. 1. Linear relationship between mean chlorophyll *a* and nutrient loading levels (nitrogen addition) for the nine mesocosms over the experimental period.

were also linearly related to nutrient loading level and thus indirectly incorporated the effects of nutrients in the models (Fig. 1).

These models were additionally compared with multiple regression models. For the seven mesocosms, the transfer function models provided a better fit to the data (as measured by the residual error) than the multiple regression models. The predictive ability of the transfer function model was subsequently tested using the replicate control systems. Most frequently, the ability to forecast using time series analysis is tested by applying the final fitted model to data obtained after the last observation used to estimate the model parameters. However, it was necessary to include all of the observations for each mesocosm in the estimation of the model parameters because of the small sample size. Consequently, the model developed for one control system was applied to the two remaining control systems, thus satisfying the need to test the model on independent data not included in the original estimation of the model.

Methods

Data

The data to be analyzed are time series of integrated hourly production, phytoplankton biomass, and light, collected biweekly, from nine mesocosms from June 1981 through September 1983. A representative sample of the time series data for a control, a low-nutrient treatment, and a high-nutrient treatment system is displayed in Fig. 2. Production was measured using the in situ ^{14}C technique (Steeman-Nielson 1952) with bottles suspended at five depths (0.1, 0.5, 1.0, 2.5, and 4.5 m) and exposed for approximately 4 h around noon (for details, see Oviatt et al. 1986b). Primary production (milligrams of carbon per cubic metre per hour) (averaged over the incubation period) was calculated following Strickland and Parsons (1972). Hourly production beneath a square metre of water surface was calculated by numerically integrating (trapezoidal rule) these values over depth.

Phytoplankton biomass was measured as chlorophyll *a* (milligrams per cubic metre) using the fluorometric method of Yentsch and Menzel (1963) as modified by Lorenzen (1966). Hourly irradiation (Einsteins per square metre per hour, PAR) was measured using an LI-COR, LI-190S quantum sensor coupled to an LI-550 printing integrator. The mean incident light over the 4-h incubation period was used in the analysis.

Analysis

A useful introduction to Box–Jenkins transfer function models is given in Jenkins (1979). A time series is a collection of observations ordered in time and shaped by both deterministic and stochastic events. In general, the analysis consists of removing deterministic trends from a series (Y_t) so that the resulting values fluctuate around a mean with constant variance (termed a stationary series). The random processes that generated the observed series can then be mathematically defined.

Box–Jenkins models can be constructed using only the information contained in the series itself (univariate models). However, to determine the manner in which light and biomass may be related to primary production, multiple input models (transfer function models) were constructed. Although information on the effects of all the inputs is already contained in the past history of production, including light and biomass in the transfer function models resulted in an equation with more predictive power. To understand the results as described in the following section, it is sufficient to describe the model as

$$(1) \qquad Y_t = U + \Sigma\, w_j\,(B)\, X_{jt} + \theta(B)/\phi(B)a_t$$

where t is the index for time, B is the backshift operator $B^jX_t = X_{t-j}$, Y_t is the original, transformed, or differenced data, U is a constant, $\phi(B)$ is an autoregressive polynomial of order p, $\theta(B)$ is a moving average polynomial of order q, a_t is the random error, X_{jt} is the jth input term, and $w_j(B)$ are the transfer function weights for the jth input series (modeled as a ratio of polynomials).

Box and Jenkins (1976) use the notation ARIMA (p,d,q) for this model, with p the order of the autoregressive component, q the order of the moving average component, and d the degree of differencing required to remove nonstationarity of the mean function.

Figure 3 shows the structure of the model. The actual fitting of the model to the observed data involved three steps. The first step, process identification, consisted of determining how many and which terms in equation 1 to retain in the final models. For transfer function models, univariate ARIMA models were first constructed for the dependent and independent variables. The univariate models for production were needed (a) so that any reduction in residual variance as a result of introducing the input variables could be measured and (b) to provide an approximation to the structure of the noise model (N_t). The univariate models for the independent variables were needed to filter both the input and output series before calculating their cross correlation function (CCF) at all lags, a process termed prewhitening. Prewhitening eliminated spuriously high cross correlations between series which were in effect a result of autocorrelation.

The second step was simultaneously estimating the parameters (w, θ, ϕ) that best fit the data. The final step was diagnostic checking to detect any shortcomings. Process iden-

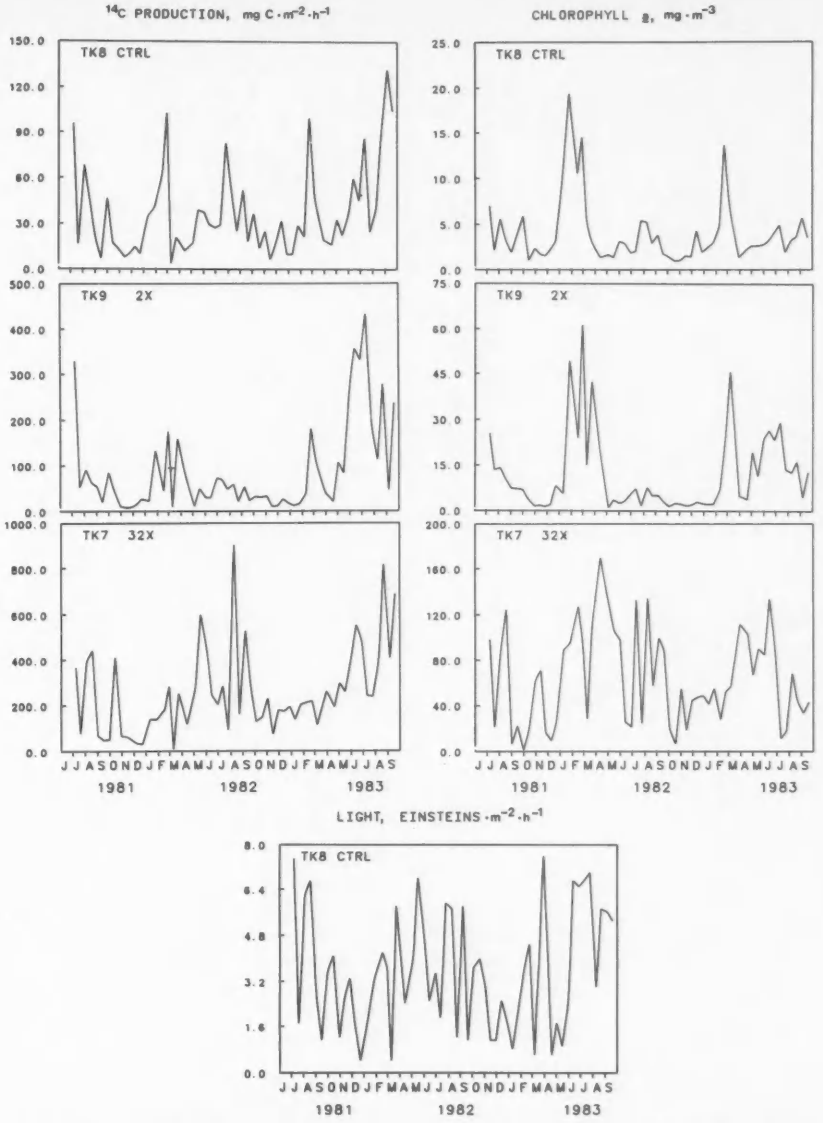
^{14}C PRODUCTION, mg C·m^{-2}·h^{-1}
CHLOROPHYLL a, mg·m^{-3}
TK8 CTRL
TK9 2X
TK7 32X
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1981
1982
1983
LIGHT, EINSTEINS·m^{-2}·h^{-1}

FIG. 2. Time series data (production and chlorophyll *a*) for a control (tank 8), a low-nutrient treatment (tank 9), and a high-nutrient treatment (tank 7) mesocosm. The time series data for light is represented by the control mesocosm.

tification, estimation, and diagnostic checking involved examining the autocorrelation (ACF) and partial autocorrelation (PACF) functions of the series and residuals, as well as the prewhitened CCFs between the input and output series. The ACF measured how much correlations there was between neighboring points in a series, while the PACF measured the strength of the relationship between time periods in a series when dependence on intervening periods was removed. The CCF provided evidence for a relationship between the input and output series at any lag. Diagnostic checking involved removal of insignificant components from the model and testing the residuals for departure from white noise. If the residuals were not equivalent with white noise, a new model was identified and the process repeated.

The data were also used to develop multiple regression models between production (the dependent variable) and biomass and light (the independent variables) for each mesocosm. The fit between these models and the time series models was compared by means of the coefficients of determination (r^2) and the variance of the residuals. For the transfer function models, the estimated variance of the a_t values, which are the one step ahead forecast error, was used. This variance is comparable with that of the regression models (Saila et al. 1979).

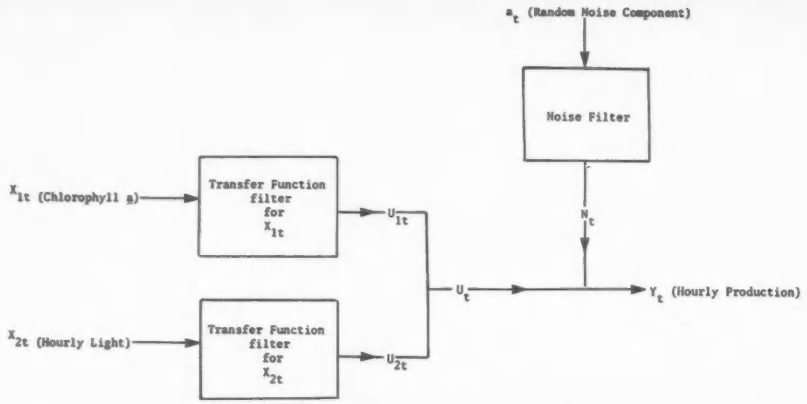

FIG. 3. Structure of production model relating hourly production (Y_t) to chlorophyll *a* (X_{1t}) and hourly light (X_{2t}). The general form of the model is $Y_t = U_{jt} + N_t$ where U_{jt} is the component of Y_t (the dependent variable) that can be explained by X_{jt} (the independent variable) and N_t is an error or noise term. U_{jt} represents the transfer function portion of the model ($\Sigma\, w_j(B)X_{jt}$) and N_t is the noise component represented itself as an autoregressive-moving-average process of a_t ($\theta(B)/\phi(B)a_t$) (see text).

TABLE 1. Univariate AR models for production (Y_t) fitted to each mesocosm (note: treatment refers to the nutrient loading level for the seven mesocosms, with C the control system). *B* in the model equation is the backshift operator and a_t is the random error.

Treatment	Fitted model	Residual variance	r^2
C	$(1 - 0.24B - 0.18B^2)Y_t = 1.94 + a_t$	0.582	0.17
1×	$(1 - 0.32B - 0.27B^2)Y_t = 1.41 + a_t$	0.565	0.27
2×	$(1 - 0.33B - 0.35B^2)Y_t = 1.29 + a_t$	0.874	0.34
4×	$(1 - 0.25B - 0.37B^2)Y_t = 1.59 + a_t$	0.843	0.25
8×	$(1 - 0.43B - 0.03B^2)Y_t = 1.95 + a_t$	0.813	0.24
16×	$(1 - 0.39B - 0.27B^2)Y_t = 1.58 + a_t$	0.768	0.36
32×	$(1 - 0.20B - 0.28B^2)Y_t = 2.71 + a_t$	0.737	0.14

TABLE 2. Univariate AR models for chlorophyll *a* (X_{1t}) fitted to each mesocosm (note: treatment refers to the nutrient loading level for the seven mesocosms, with C the control system). *B* in the model equation is the backshift operator and a_t is the random error.

Treatment	Fitted model	Residual variance	r^2
C	$(1 - 0.48B)(1 + 0.27B^{19})X_{1t} = 0.72 + a_t$	0.324	0.35
1×	$(1 - 0.60B)(1 + 0.26B^{20})X_{1t} = 0.72 + a_t$	0.734	0.42
2×	$(1 - 0.60B)(1 + 0.21B^{20})X_{1t} = 0.92 + a_t$	0.687	0.44
4×	$(1 - 0.60B)(1 - 0.24B^{26})X_{1t} = 0.71 + a_t$	0.936	0.49
8×	$(1 - 0.70B)(1 - 0.31B^{25})X_{1t} = 0.34 + a_t$	0.693	0.57
16×	$(1 - 0.74B)(1 - 0.54B^{24})X_{1t} = 0.36 + a_t$	0.601	0.68
32×	$(1 - 0.25B)(1 - 0.12B^{26})X_{1t} = 2.51 + a_t$	0.854	0.17

Results

Univariate ARIMA models were first constructed for the natural logarithmically transformed output (production) and input variables (chlorophyll *a* and light). An approximately linear relationship between the ranges and means for the output and both input variables suggested the need for natural logarithmic transformations (Jenkins 1979). For hourly production, the ACF and PACF for the seven mesocosms all exhibited a similar pattern (see Fig. 4 for a representative sample). The damped sinusoidal decay pattern of the ACF is indicative of a stationary autoregressive model. The order of the model is indicated by the PACF. There were two significant values for the PACF at lags 1 and 2, suggesting a second-order autoregressive model, AR(2,0), i.e. one in which the current value of production depended on the past two values. Table 1 shows the fitted univariate models for each mesocosm and the residual variance. For all mesocosms, neither the means nor any of the ACF and PACF of the residuals were significant, indicating that the models were acceptable.

The decay patterns for the ACF for chlorophyll *a* were also typical of stationary autoregressive models. For each treat-

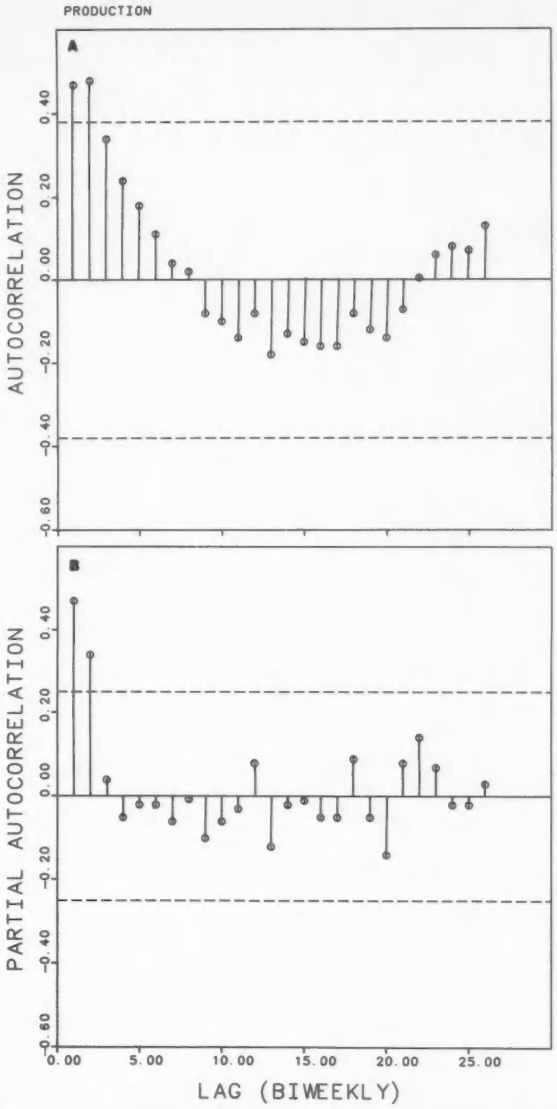

FIG. 4. (A) Estimated autocorrelation and (B) partial autocorrelation functions to lag 26 for the logarithmically transformed production data for the 2× mesocosm (tank 9) together with their two standard error limits (broken lines).

ment, a significant peak was observed at approximately lag 26 (varying from lag 19 to lag 26), suggesting a seasonal pattern. The PACF had significant values at lags 1 and ~26, indicating that chlorophyll *a* for all treatments was best described by a first-order autoregressive model with a seasonal component (Table 2). The mean of the residuals for all treatments was not significant.

The ACF and PACF for light had a single significant value at lag 15, indicating a seasonal autoregressive model with a semiannual cycle. The data for all treatments were fit to a single model:

$$(2)\quad (1 + 0.40B^{15})X_{2t} = 1.38 + a_t$$

with a residual variance of 0.58 ($r^2 = 0.15$). The means of the ACF and PACF of the residuals were insignificant.

The univariate models for the input variables were used to calculate prewhitened CCFs with production. For chlorophyll *a*, this function had a large positive value at lag zero for all mesocosms. For some treatments (2×, 4×, 16×, and 32×), additional significant values occurred at lags 1 and 2. Based on these findings, two models were hypothesized for the relationship between Y_t and X_{1t}:

$$(3)\quad Y_t = w_0X_{1t} + N_t$$

$$(4)\quad Y_t = w_0X_{1t} - w_1X_{1t-1} - w_2X_{1t-2} + N_t.$$

Subsequent analysis revealed that the second model (equation 4) was overspecified and the models for the 2×, 4×, 16×, and 32× treatments were finally represented as

$$(5)\quad Y_t = w_0X_{1t} - w_1X_{1t-1} + N_t.$$

The univariate models for Y_t (Table 1) were then used as the first approximation to the noise models, N_t, for the seven mesocosms. Thus, the noise models were represented as

$$(6)\quad (1 - \phi_1B - \phi_2B^2)N_t = a_t.$$

The fitted single input (biomass, X_{1t}) transfer function – noise models for the seven mesocosms are included in Table 3.

The CCFs between production and light all had large positive values at zero lag and were small thereafter, suggesting a relationship between Y_t and X_{2t} of the form

$$(7)\quad Y_t = w_0X_{2t} + N_t.$$

The noise portion of the model was again approximated by the univariate models for Y_t. The fitted models for the single input (light, X_{2t}) transfer function models are seen in Table 3.

A final model was fitted for each mesocosm using both biomass and light as input variables (Table 3). All parameters were estimated simultaneously. Based on diagnostic tests, there was no evidence of model inadequacy for the seven models. It can be seen from Tables 1 and 3 that the residual variance for the single input model was always lower than for the univariate model and that the residual variance for the multiple input model was always lowest (Table 3). Furthermore, for most mesocosms, a greater portion of the residual variance was accounted for by biomass as compared with light (Table 3). Chlorophyll *a*, in nutrient-rich estuaries, integrates the effects of several factors and, while not necessarily a causal factor for production, greatly improves the predictive ability of the model.

For comparative purposes, the data were then used to develop multiple regression models for the seven mesocosms using general linear least squares regression techniques (Table 4). Tables 3 and 4 show the goodness of fit for the two types of models (multiple regression and time series) based on the coefficients of determination and the variance of the residuals.

Discussion

Univariate Models

Production

The univariate models for production revealed that it would be difficult to predict the future productivity of a system based

TABLE 3. Single input and multiple input transfer function models relating production (Y_t) to chlorophyll *a* (X_{1t}) and light (X_{2t}) for the seven mesocosms (note: Trt refers to the nutrient treatment level.

Trt	Model type	Fitted model	Residual variance	r^2
C	Single input: X_{1t}	$Y_t = 2.56 + 0.72X_{1t} + (1/(1 - 0.25B - 0.23B^2))a_t$	0.388	0.40
	Single input: X_{2t}	$Y_t = 2.74 + 0.60X_{2t} + (1/(1 - 0.24B - 0.11B^2))a_t$	0.356	0.45
	Two inputs: X_{1t}, X_{2t}	$Y_t = 2.10 + 0.63X_{1t} + 0.54X_{2t} + (1/(1 - 0.24B - 0.15B^2))a_t$	0.210	0.68
1×	Single input: X_{1t}	$Y_t = 2.62 + 0.53X_{1t} + (1/(1 - 0.15B - 0.31B^2))a_t$	0.337	0.54
	Single input: X_{2t}	$Y_t = 3.07 + 0.32X_{2t} + (1/(1 - 0.33B - 0.16B^2))a_t$	0.504	0.32
	Two inputs: X_{1t}, X_{2t}	$Y_t = 2.08 + 0.56X_{1t} + 0.48X_{2t} + (1/(1 - 0.13B - 0.05B^2))a_t$	0.221	0.71
2×	Single input: X_{1t}	$Y_t = 2.45 + (0.84 - 0.10B)X_{1t} + (1/(1 - 0.31B - 0.37B^2))a_t$	0.285	0.77
	Single input: X_{2t}	$Y_t = 3.46 + 0.54X_{2t} + (1/(1 - 0.37B - 0.28B^2))a_t$	0.619	0.49
	Two inputs: X_{1t}, X_{2t}	$Y_t = 2.03 + (0.82 - 0.09B)X_{1t} + 0.45X_{2t} + (1/(1 - 0.44B - 0.25B^2))a_t$	0.144	0.88
4×	Single input: X_{1t}	$Y_t = 2.67 + (0.58 - 0.02B)X_{1t} + (1/(1 - 0.19B - 0.29B^2))a_t$	0.428	0.60
	Single input: X_{2t}	$Y_t = 3.49 + 0.60X_{2t} + (1/(1 - 0.39B - 0.15B^2))a_t$	0.588	0.45
	Two inputs: X_{1t}, X_{2t}	$Y_t = 2.27 + (0.58 - 0.05B)X_{1t} + 0.54X_{2t} + (1/(1 - 0.17B - 0.17B^2))a_t$	0.255	0.79
8×	Single input: X_{1t}	$Y_t = 2.67 + 0.60X_{1t} + (1/(1 - 0.08B - 0.01B^2))a_t$	0.464	0.54
	Single input: X_{2t}	$Y_t = 2.97 + 0.57X_{2t} + (1/(1 - 0.44B - 0.01B^2))a_t$	0.622	0.38
	Two inputs: X_{1t}, X_{2t}	$Y_t = 2.04 + 0.58X_{1t} + 0.62X_{2t} + (1/(1 - 0.19B - 0.10B^2))a_t$	0.257	0.75
16×	Single input: X_{1t}	$Y_t = 2.76 + (0.61 - 0.02B)X_{1t} + (1/(1 - 0.14B - 0.11B^2))a_t$	0.446	0.60
	Single input: X_{2t}	$Y_t = 3.94 + 0.62X_{2t} + (1/(1 - 0.61B - 0.09B^2))a_t$	0.487	0.57
	Two inputs: X_{1t}, X_{2t}	$Y_t = 2.31 + (0.64 - 0.06B)X_{1t} + 0.59X_{2t} + (1/(1 - 0.14B - 0.15B^2))a_t$	0.227	0.80
32×	Single input: X_{1t}	$Y_t = 3.93 + (0.48 - 0.14B)X_{1t} + (1/(1 - 0.31B - 0.27B^2))a_t$	0.480	0.41
	Single input: X_{2t}	$Y_t = 4.60 + 0.64X_{2t} + (1/(1 - 0.20B - 0.27B^2))a_t$	0.427	0.48
	Two inputs: X_{1t}, X_{2t}	$Y_t = 3.57 + (0.44 - 0.15B)X_{1t} + 0.59X_{2t} + (1/(1 - 0.35B - 0.29B^2))a_t$	0.240	0.71

TABLE 4. Multiple regression models for the seven mesocosms relating the dependent variable production (Y) to the independent variables chlorophyll *a* (X_1) and light (X_2) (note: all variables have been natural logarithmically transformed; Trt refers to nutrient treatment levels).

Trt	Fitted model	r^2
C	$Y = 2.08 + 0.58X_{1t} + 0.60X_{2t}$	0.64
1×	$Y = 2.07 + 0.55X_{1t} + 0.51X_{2t}$	0.69
2×	$Y = 1.88 + 0.75X_{1t} + 0.57X_{2t}$	0.81
4×	$Y = 2.17 + 0.56X_{1t} + 0.61X_{2t}$	0.74
8×	$Y = 2.06 + 0.58X_{1t} + 0.60X_{2t}$	0.72
16×	$Y = 2.25 + 0.60X_{1t} + 0.58X_{2t}$	0.77
32×	$Y = 2.95 + 0.42X_{1t} + 0.66X_{2t}$	0.59

on its past production alone. At most, 36% of the variation in production could be explained by its past history. Statistically, the structure of the random processes that generated the production series was specified as a second-order autoregressive process for all mesocosms. For most cases, production in the current time period depended to a greater extent on the immediately preceding period and to a lesser extent on the period prior to this. This suggested that the physiological characteristics of the phytoplankton populations varied over a 4- to 6-wk time scale and corresponded with the time scale for species succession (Cote and Platt 1983). The absence of a yearly productivity cycle can be explained by Durbin et al.'s (1975) finding that while nanoplankton predominate in summer and netplankton in winter, the contributions to annual production by the two size classes in Narragansett Bay are essentially equal.

Chlorophyll a *and light*

Even though the chlorophyll *a* maxima do not match between mesocosms and the mean levels vary between treatments, the process that generated these time series in all mesocosms was the same and can be described as a seasonal AR model. The approximately 26-wk period (19–26 wk) suggested a yearly seasonal model. The seasonal component is related to the winter diatom bloom characteristic of Narragansett Bay. This bloom, which occurred every year of a 14-yr study, usually peaks in January, but has been as late as March (1964, 1969) and April (1966) (Smayda 1976). The variation in the seasonal lag among mesocosms (19–26 wk) reflected this year-to-year variation in the occurrence of the major annual phytoplankton bloom.

The mean hourly light in the 4 h around noon was described by a seasonal model with a lag of 15. The univariate model for light explained only 15% of the variation in the series and emphasized the random nature of the controlling variable, cloud cover.

Transfer Function Models

A central objective of the modeling procedure was the elucidation of the dynamic system response (transfer function) which translated the time series of the forcing variables (light, biomass) into that of the variable of interest (production). The fact that the CCFs between both inputs and production have their maximum values at lag 0 is a significant finding. This model indicated that the current values of chlorophyll *a* and light have an effect on the current values of production. It also implied that a change in the controlling factors will produce a rapid response in production. Given the observed relationship between chlorophyll *a* and nutrient loading level (Fig. 1), this information should be of use to environmental managers. Cole and Cloern (1984), Bruno et al. (1983), and Cole et al. (1986) similarly noted that temporal variations in chlorophyll *a* and light generally coincided with variations in productivity.

The final transfer function models for all mesocosms (Table 3) were very similar, with the major difference being the

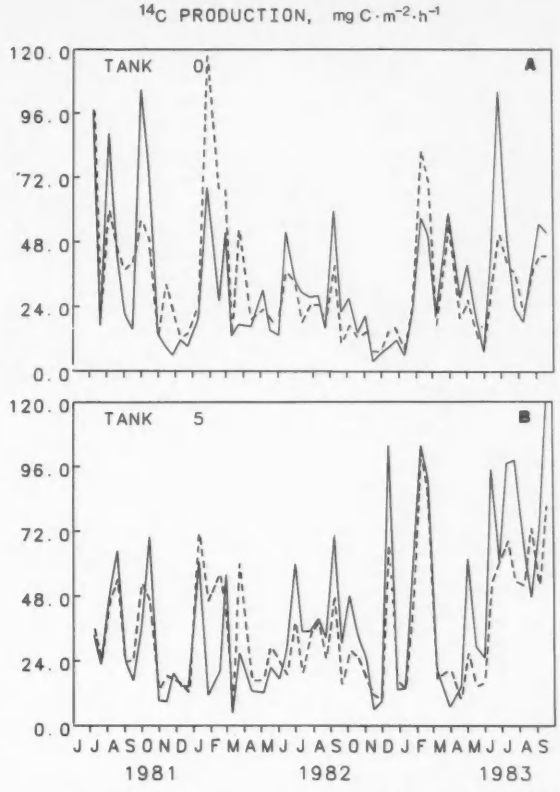

FIG. 5. Comparison between the measured hourly production (solid line) and the predicted production (broken line) for (A) tank 0 and (B) tank 5 (controls) determined from the transfer function model for tank 8 (control). Predictions are multistep forecasts with coefficients of determination of 0.69 for tank 0 and 0.71 for tank 5.

incorporation of a second parameter in the function between biomass (X_{1t}) and production (Y_t) for the 2×, 4×, 16×, and 32× treatments. As indicated by the model parameters (Table 3), production in these mesocosms was always more influenced by chlorophyll *a* in the current period than in the preceding period. Additionally, these treatments had the highest mean biomass levels over the experimental period. A change in the factors controlling photosynthesis thus produced an effect of greater duration in the higher biomass treatments. Since nutrient loading levels were linearly related to phytoplankton biomass (Fig. 1), these results suggested that enhanced nutrients extended the duration of phytoplankton production events. Kremer and Nixon (1978) corroboratively reported extended bloom periods for simulated biomass levels in Narragansett Bay along an increasing nutrient gradient.

An important point is that the underlying processes were essentially the same between mesocosms even though the actual time series looked different between treatments. This suggested that the above approach may be valid for use in nutrient-rich estuarine systems where production does not reach saturation as a result of nutrient limitation.

Forecasting

For all mesocosms, the transfer function models provided a better fit to the data (than the multiple regression models) based on the variance of the residuals (Tables 3 and 4). However, there was at most a 12% increase in the coefficient of determination between the two model types. Based on the small but significant increase in the fit of the model, it was decided to further evaluate the transfer function models.

An important check of any model is to compare predicted values with actual data not used in fitting the model. As noted previously, the ideal situation is to extend the forecast beyond the last observation used in parameter estimation. Since all of the data for each mesocosm were used in the fitting procedure, the model was tested on the replicate control systems. Forecasts for tank 0 and tank 5 were made using the model parameters estimated with the data from the tank 8 control (Table 3). The detransformed hourly production forecasts for both systems are compared with the actual data (Fig. 5). From Fig. 5 it is clear that the transfer function model does have predictive ability. The residual variances for the predictive models were calculated (tk0 = 0.235, tk5 = 0.231) and compared favorably with the residual variance for the original fitted model (tk8 = 0.210). While this approach did not allow the models for the treatment tanks to be tested, it did indicate a potential ability for successful forecasting.

Forecasting production is of central importance in estuarine environments because of its role in supporting many food webs (Boynton et al. 1982). The ability to forecast from readily measured environmental variables, such as biomass and light, should aid environmental managers seeking to control the threat of "cultural" eutrophication. Additionally, reliably predicting production has clear logistic advantages over measurement, particularly when high-resolution (in space or time) data on primary production are needed. Cote and Platt (1983) expressed concern over the further development of predictive production models because of the importance of physical transients in the short-term dynamics of a system. The possibility of incorporating random environmental events into time series models (Box and Jenkins 1976; Mendelssohn 1981) is an added advantage when using this type of analysis.

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Binational Management of Pacific Hake (*Merluccius productus*): A Stochastic Modeling Approach

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We use an age-structured stochastic recruitment model to examine a stock managed by two nations: the Pacific Hake (*Merluccius productus*) fishery. The model computes the mean and variance in stock and yield and the probability (risk) that the stock falls into a critically low condition. An optimization algorithm finds effort quotas that maximize expected yield over a short-term planning horizon while constraining the risk of critically low stock conditions. Yields produced exceed those of constant effort alternatives, but with year-to-year fluctuations in fishing effort including fishery closures. These occur in different years for the United States and Canadian fisheries depending on the condition of the stock and the incoming year class. Binational management of fishing effort is also presented as a two-person game with a weighted difference between fishery catch and effort as payoff. Nash (rational players), maxi–min (self-protecting), and Pareto (cooperative optimizing) strategies are examined. There are striking shifts in relative effort between United States and Canadian fisheries as the cost of effort changes relative to catch. This approach shows potential benefits to both players in playing a long-term cooperative strategy.

Les auteurs ont utilisé un modèle de recrutement stochastique structuré selon les âges pour étudier un stock géré par deux pays, soit le merlu du Pacifique (*Merluccius productus*). Le modèle évalue la moyenne et la variance du stock et du rendement et la probabilité (risque) que le stock chute à une condition critique. Un algorithme d'optimisation permet de calculer l'effort qui maximise le rendement attendu au cours d'un horizon de planification à court terme tout en limitant le risque de conditions critiquement faibles du stock. Les rendements obtenus sont supérieurs à ceux générés par des modèles à effort constant quoiqu'ils montrent des fluctuations d'une année à l'autre pour ce qui est de l'effort de pêche y compris des fermetures. Selon la condition du stock et l'importance de la classe d'âge suivante, ces fermetures ont lieu différentes années pour les pêches américaines et canadiennes. On présente la gestion binationale de l'effort de pêche comme un jeu entre deux personnes dont l'enjeu est une différence pondérée entre les prises et l'effort de chaque pays. On examine ainsi les stratégies de Nash (joueurs rationnels), maxi–min (autoprotectrice) et Pareto (optimisation coopérative). On observe des déplacements marqués de l'effort relatif entre les pêches américaines et canadiennes selon que le coût de l'effort change par rapport aux prises. Cette approche révèle des avantages potentiels pour les deux joueurs dans une stratégie coopérative à long terme.

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Little attention has been paid in the fisheries literature to the effect on a fish stock of having a single stock managed separately by two or more countries. There are, however, many such stocks in the world. Major fisheries such as the George's Bank fishery, the North Pacific salmon and halibut fisheries, the North Sea fishery, and the Benguela current fishery have stocks that move between the territorial waters of several countries. Sometimes the allocation of the fishery between vessels of the various countries involved has been settled by treaty, such as with the halibut and salmon fishery allocation between United States and Canadian registered vessels. Most often, however, a laissez-faire approach is adopted in which vessels fish in their own territorial waters without consideration or concern for the allocation problem. This laissez-faire approach also reflects the lack of information with regard to stock migrations between territorial waters and to the effect that fishing in one area has on catch in another.

We have examined the question of fishing effort allocation between territorial waters in the Pacific hake (*Merluccius productus*). This species spawns in southern California and northern Mexico (Francis 1983; Swartzman et al. 1983) during January and migrates north during the spring. The northern

migration is subject to fishing pressure largely by a foreign fleet that has, in the last few years, converted almost entirely to a joint-venture fishery in which United States and Canadian boats fish within their territorial waters and unload on foreign processor vessels.

As corroborated by catch data, it is known that the larger fish in this stock tend to migrate further north (Francis 1983). This is important to our analysis in that the catchability (relative availability) of the smaller, younger fish is much less in the Canadian than in the United States managed fishery. On first reflection, this appears to put control of the stock in the effort generated by the United States managed fishery because fish become available to that fishery before they are fished in Canada. However, Pacific hake fecundity (egg production) appears to be a nonlinear function of weight (S. MacFarland, Pacific Biological Station, Nanaimo, B.C., unpubl. data). This increases the contribution to total fecundity by the older stock above its proportion in the population and might result in a drastic reduction in fecund stock if the younger stock is overfished (because overfishing skews the age structure towards younger fish). Thus, it is to the advantage of managers of the hake stock from both nations to protect the stock from overfishing.

The present hake stock is primarily a joint venture fishery, largely because the United States and Canadian domestic fisheries have developed neither the market nor an effective method for processing these fish. This fish carries a myxosporea parasite (*Kudoa paniformis*) that, through proteolytic activity in the muscle tissue, can lead to serious degradation of the flesh texture after death. This makes rapid processing of the fish after capture necessary, which consequently prevents the largely land-based United States and Canadian processing industries from handling this species. Should a cure or alternative processing method be developed, this large fishery (around 200 000 metric tons (t) annually) could burgeon into a major domestic fishery, as it has with the related South African species (*Merluccius merluccius*).

Another important feature of the hake stock is the linkage between recruitment success and Eckmann transport (upwelling of cooler deep waters due to steady offshore winds) on the hake spawning grounds (Bailey 1981). Recruitment in hake is highly variable and it appears that both average recruitment and recruitment variability are higher when Eckmann transport is low (warmer sea surface temperature) at the time an age class is spawned, and the converse is true in years of high Eckmann transport (cooler sea surface temperature) (Swartzman et al. 1983). There is a 3-yr lag between the time of spawning and recruitment into the fishery. Thus, knowing surface temperatures over the last 3 yr gives some foreknowledge about expected recruitment over the next 3 yr, which can help in planning quotas over a period longer than a single year.

The high variability in hake recruitment and its linkage to sea surface temperatures at the time of spawning, the longevity of this stock, the difference in catchability at age between the United States and Canadian managed fishery, and the egg production being a nonlinear function of fish weight all suggest using an age-structured model with a stochastic stock–recruit relationship that depends on the spawning time sea surface temperature and splits the catch and effort between the Canadian and United States managed fisheries.

The model we use here is adapted from earlier age-structured stochastic recruitment models (Getz and Swartzman 1981; Swartzman et al. 1983) to include the multinational nature of hake stock management.

Multinational management of the fishery is addressed here through both a short-term management and an equilibrium approach. In the short-term approach, we develop an algorithm for choosing the annual effort (or yield) quota such as to maximize an objective function (usually total yield or profit) over a multiyear (5- to 10-yr) planning horizon. A constraint is imposed on the problem to limit the probability to less than 5% (or some other appropriate risk level) that the stock falls below an a priori selected threshold level over the planning horizon. This limits the risk that the fishery may collapse from overexploitation. Another constraint requires the stock to return to the expected equilibrium stock level at the end of the planning horizon.

The equilibrium approach places multinational management of the hake stock into a two-person game context. In this context the two managing countries are seen as having some long-term objective relating to either yield or profit, which can be envisioned as a game in which the outcome of a given long-term effort strategy played by both countries results in an expected payoff (yield or profit) to each country. The resultant payoff depends on the effort choice of both players. Three concepts from game theory — the Nash, maxi–min, and Pareto strategies — are used to compare payoffs for strategies of rational competition, self-protection, and cooperation.

Model Parameters and Behavior

The model is an age-structured population dynamics model having its state described by the mean and variance of the population in each age class and the covariances between the age classes. The population's state also includes the mean and variance in fecund stock, which is assumed to be gamma distributed. This assumption was made because (1) results from an earlier model, which treated the age class distribution as discrete random variables (rather than as a mean and variance as in this model), gave stock probability distributions that were close to gamma (Getz and Swartzman 1981). (2) the mathematics for projecting the mean and variance in age classes and stock into the future are tractable with a gamma distribution, and (3) the gamma distribution is close to the lognormal distribution that Tuljapurkar (1982) has shown that the equilibrium stock approaches in a stochastic Leslie matrix model without a stock–recruit relationship. From these parameters and the gamma assumption, the probability or risk that the stock is in an unacceptably low condition can be computed. Recruitment in this stock is given by the mean and variance as a function of stock level, with the mean and variance curves being conditional on the Eckmann transport conditions at the time of spawning (in turn measured by the sea surface temperature in the Los Angeles Bight). The model allows the mean and variance in yield to be calculated depending on the effort in both United States and Canadian fisheries, the model parameters, and the state of the population at the start of the fishing season. The details of the model are given in Appendix 1.

This model includes variance in year class strength explicitly, in contrast with a Monte Carle simulation approach. The latter approach includes variance implicitly by sampling from parameters in the model that introduce variability into model output, but treating outputs of each run as deterministic. In this model the major source of variability is in the stock–

TABLE 1. Parameter values used in sumulation runs.

Parameter	Age 3	4	5	6	7	8	9	10	11	12
Natural mortality rate (m_i)	0.2095	0.1952	0.2570	0.3570	0.4570	0.5570	0.6570	0.7570	0.7570	0.8570
Catchability coefficient										
U.S. (q_i^a)	0.0063	0.0203	0.0298	0.0418	0.0539	0.0987	0.1294	0.1504	0.2770	0.2770
Canada (q_i^c)	0.0000	0.0000	0.0519	0.0541	0.0779	0.0927	0.1766	0.3789	0.7624	0.7624
Maturity coefficient (c_i)	0.5	0.75	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Weight at age (w_i) (kg)	0.433	0.545	0.663	0.769	0.855	0.947	1.023	1.078	1.134	1.205
Initial number at age (μ_i (0)) (billions)	2.200	1.650	1.190	0.917	0.458	0.275	0.092	0.031	0.009	0.003
Initial SD at age (σ_i (0)) (billions)	0.240	0.180	0.130	0.100	0.050	0.030	0.010	0.003	0.001	0.003

Stock-recruitment	Parameters: Warm	Cold
R_{max}	0.82×10^9	0.125×10^9
α	1.22×10^{-14}	1.22×10^{-14}
Coefficient of variation	1.066	0.68

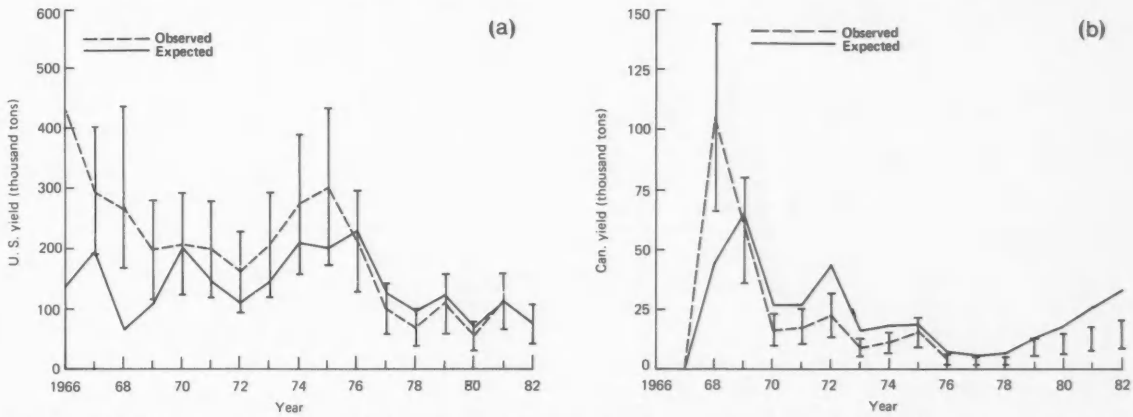

FIG. 1. Simulated expected yield for (a) the United States and (b) the Canadian managed fisheries from 1966 to 1982. Error bars of ±1 SD are drawn around the expected yields.

recruit relationship and how it is affected by weather conditions at the time of hake spawning. The major advantage of using a model having explicit, rather than implicit, computation of risk (to stock collapse) is that management decisions relative to risk can be made within a single run of the model. Because these management decisions (regarding setting annual effort quotas) affect future model performance, we have a tool that permits something that cannot be done with a deterministic approach (which ignores explicit risk) and a Monte Carlo approach (which requires many runs to be made before the best expected policy can be calculated).

The parameters for the model applied to Pacific hake (Table 1) have been estimated from the data as described in Swartzman et al. (1983). Canadian and United States catchabilities were estimated using cohort analysis (Pope 1972) with data from Francis (1985) and from U.S. National Marine Fishery Service survey data for 1977, 1980, and 1983. Stock–recruit parameters were estimated using regressions

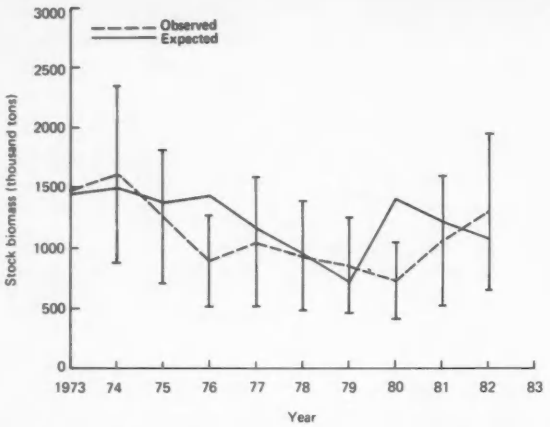

FIG. 2. Simulated expected stock biomass compared with stock estimates obtained from cohort analysis from 1973 to 1982. Error bars of ±1 SD are drawn around the model predictions.

from data given in Swartzman et al. (1983). Figures 1 and 2 compare expected yield and stock from a simulation using surface sea temperatures for the Los Angeles Bight from 1933 to 1982 with available data, for those years for which such data are available. Remember that sea surface temperature, as an index of upwelling, determines the form of the curves for mean and variance in recruitment as a function of stock. Yield for both the United States and Canadian managed fisheries are compared, beginning in 1966 when the foreign fleet hake fishery began. Stock estimates from 1973 to 1980 are compared in Fig. 2 with model output. The stock estimates were obtained from catch at age data using cohort analysis (Pope 1972).

These figures show that the model is able to simulate the essential dynamics of the fishery, although there are biases in both United States and Canadian catch predictions. Although the data on which the parameters are based are too limited to place great confidence in the predictive ability of the model, the model compares well with the data. The error bounds give some idea about how variance is propagated by a model like this, with variance being less in time of less effort. Sources of error in the data, especially for early years, are discussed in Swartzman et al. (1983).

Short-Term Management

The annual catch quotas set by groundfish management teams in the United States and Canada are done in isolation of each other. However, the fishing effort in the United States can have a significant effect on catches in both the United States and Canada although the reverse is less clear.

We used the stochastic age-structured model as a tool to develop a policy for short-term (5–10 yr) fishery management that considers the binational nature of the fishery management. This policy reflects a manager's objective of setting quotas to maximize, say, yield over a fixed length planning horizon while protecting the stock from overfishing.

For this short-term policy, we considered only the case of cooperation between the two fishery management groups, assuming that the managers have complete control over effort in the fishery. Fishing effort is transformed into an expected annual yield by the model. Notice that the variance in yield is derived in the model from variance in recruitment (a stochastic stock–recruit relationship), not variance in catch-per-unit-effort. We have assumed that the major source of variance in this fish stock is in its recruitment and have put our emphasis there.

Our policy is encoded into a computer algorithm. It starts with the present mean and variance for each age class in the fishery and the sea surface temperatures over the last 3 yr (3 yr are used because there is a 3-yr lag in hake from the time of spawning to recruitment, i.e. $r = 3$; see Appendix 1) and sets effort (yield) quotas over an h-yr planning horizon (h ranges from 5 to 10 yr) so as to maximize a weighted linear function of United States and Canadian yield over the planning period. As we will show, the "optimal" solution is not a true optimum because the effort space (the vector of efforts over the h-yr planning horizon) is constrained. These constraints are necessary to achieve the policy within a reasonable computation time. The algorithm is computationally intensive. The following specific constraints are imposed on the optimization algorithm.

(1) The probability that the stock falls below a dangerous threshold level is less than 5% (or some other risk probability) over the planning period. This constraint was chosen to reduce the risk of drastic stock reduction to a level related to recruitment under a string of cold surface temperature (poor recruitment) years.

(2) The expected stock level must be above the maximum equilibrium sustainable yield (MESY) level at the end of the h-yr planning period. This constraint assures that the stock will be left in good condition at the end of the planning period (see Getz 1985). The MESY is obtained by running the model to equilibrium at various effort levels with average sea surface temperature conditions (use the stock–recruit curve corresponding to the sum of those for cold and warm years weighted by their frequency of occurrence during the 50 yr of available sea surface temperature data) and choosing the effort combination giving the maximum expected equilibrium yield.

(3) The effort is constrained to be less than some maximum $v^a_{\max}$ for the United States and $v^c_{\max}$ for the Canadian managed fisheries. This constraint places the allowable efforts within the observed range of efforts and prevents efforts well beyond the present fleet capacity.

The policy algorithm

The algorithm searches effort space for the combination of efforts for the planning years $1, \ldots, h$, $\mathbf{v}^a = (v_1{}^a, \ldots, v_h{}^a)$, and $\mathbf{v}^c = (v_1{}^c, \ldots v_h{}^c)$ that maximize the following objective function:

$$J = \sum_{k=1}^{h} \beta_1 \cdot \mu_y{}^a(k) + \beta_2 \cdot \mu_y{}^c(k)$$

where β_1 = weight on United States yield in objective function, β_2 = weight on Canadian yield in objective function, $\mu_y{}^a(k)$ = expected United States yield in planning year k, and $\mu_y{}^c(k)$ = expected Canadian yield in planning year k.

Finding the true optimal solution would require searching a $2h$-dimensional space of United States and Canadian yields over all years of the planning period — an option we considered computationally intractable. As an alternative, we limited the search to a two-dimensional space by constraining the allowable United States and Canadian yield vectors. The general idea is to represent changes in effort over the h-yr planning

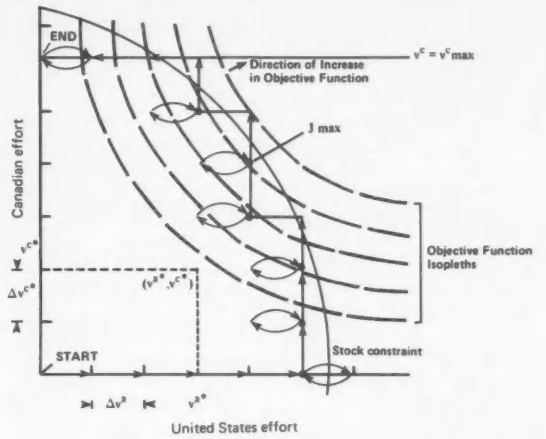

FIG. 3. Illustration of the optimal effort search algorithm with the United States and Canadian efforts as axes. Search begins at a (0, 0) effort combination and increases United States effort in steps of Δv^a until a stock constraint is violated. Canadian effort is then increased by Δv^c and United States effort is reduced until a feasible effort combination is found. This step continues until United States effort is reduced to 0.0 or the Canadian effort constraint v^c_{max} is encountered. The highest value of the objective function J is chosen for each possible Canadian effort (each row). The MESY effort point (v^{a*}, v^{c*}) controls the setting of effort over the h-yr planning horizon.

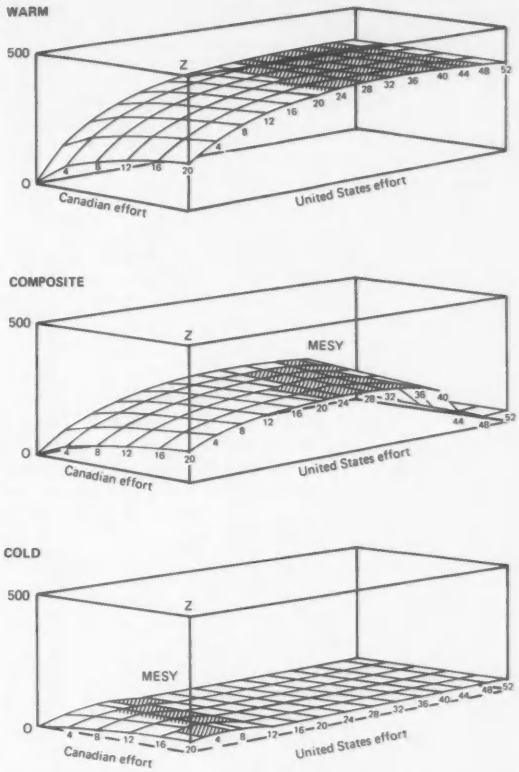

FIG. 4. Expected equilibrium yield as a function of United States and Canadian effort level for warm, composite (average), and cold sea surface temperatures at the time of spawning. The effort levels leading to MESY can be seen from these graphs for the cold and composite cases. No MESY points exist for the warm temperature case. The shaded region in each case depicts efforts close to MESY. Efforts are in units of thousands of vessel-days.

horizon not by changes in $2h$-dimensional effort vectors, but as changes imposed in a constrained fashion on all h annual efforts for both the United States and Canadian fisheries. These constrained effort changes depend on whether the effort for the fishery is above or below the MESY effort level. If above, changes in effort are made only to the first year's effort, while if below MESY, effort changes are distributed equally among the h yr of the planning horizon. This search algorithm is based on exploiting the fishery when the stock is strong (above MESY conditions) and reducing effort when the stock is weak. This policy has been shown, in another context, to produce close to optimal yields (see Getz et al. 1987).

The algorithm is illustrated in Fig. 3. The $2h$-dimensional effort space has been reduced to a two-dimensional effort space. The algorithm systematically searches the effort space for the United States and Canadian effort combination that gives the largest J value without violating any of the constraints. It is described in detail in Appendix 2.

Several parameters whose values can influence the annual quotas produced must be set in the algorithm. These include the MESY effort levels, v^{a*} and v^{c*} (the effort level used when stock levels correspond to MESY conditions), the number of years in the planning horizon h, the unit of United States and Canadian effort used in the search, Δv^a and Δv^c, and a probability associated with the risk of the stock falling below the stock (egg) "''risk threshold."'' Lacking the guidance of prior studies on how to choose values for these parameters, we adopted the following strategy.

(1) The MESY effort was set to the United States–Canadian effort combination producing MESY under "average" sea surface temperature conditions. The parameters used in the stock–recruit relationship $R_{max}(T)$ and $\alpha(T)$ for the average sea surface temperature conditions were the sum of the corresponding values for warm and cold surface temperatures conditions weighted by the probability of warm (0.497) and cold (0.503) years, respectively. The temperature probabilities were obtained as a frequency estimate from the 1933–82 Los Angeles Bight sea surface temperature data set (see Swartzman et al. 1983). The MESY values used here were 28 000 and 8000 vessel-days for United States and Canadian fisheries, respectively. This can be seen in Fig. 4 which shows the plot of yield against United States and Canadian effort for equilibrium runs of warm, cold, and composite (average) sea surface temperature conditions.

(2) We did not let the probability that the stock falls below the stock risk threshold become higher than some target probability. This target probability was set as the probability that the stock is below this threshold in simulations leading to MESY for cold sea surface conditions. To explain the rationale, we turn to Fig. 4. Notice that the MESY efforts for cold years are much lower than for either composite or warm years. If the stock should fall into the lowest category and a string of cold years should follow, management of the fishery around the much higher effort levels of the average MESY would push the stock and yield yet lower. Thus, the risk probability parameter value is chosen to protect the stock against a string of poor recruitment years with stock being managed with criteria set

TABLE 2. Estimated yield and stock for two short-term hake management alternatives compared with two constant effort cases.

Case	Average yield (kt)			Average stock (kt)	Minimum stock (kt)
	U.S.	Canada	Total		
(a) Risk ($p \leq 0.025$)	155	36	191	909	494
(b) Risk ($p \leq 0.05$)	170	25	195	717	417
(c) Constant effort (MESY)	148	13	161	603	270
(d) Constant effort (max)	156	33	189	1032	422

based on average years. The relevant probability value was 0.025. We also tried a probability of 0.05 as an analogue to a commonly chosen value for the type I error in statistics.

(3) The planning period was set to 5 yr because this was long enough to allow recruitment, resulting from fishing conditions in the first year to affect the stock in the later years, but short enough so that the weather conditions over the last 3 yr (which affect recruitment over the next 3 yr) would have a significant impact on the policy. Longer planning horizons would require recruitment in later years to depend on average weather conditions (because nothing more than the average expected recruitment can be estimated after 3 yr).

(4) The effort unit was selected to be 2000 vessel-days. It was chosen because it is large enough to ensure that the search algorithm would have a small number of nodes but small enough to ensure that one unit of change in effort would not produce large changes in yield.

(5) Several cases could be studied using different objective function weightings. The weightings $\beta_1 = 1.0$ and $\beta_2 = 1.0$ reflect an equity of importance policy. Other values reflect a United States centered fishery ($\beta_1 = 1.0$, $\beta_2 = 0.0$) or a Canadian centered fishery ($\beta_1 = 0.0$, $\beta_2 = 0.0$). For all runs in this paper, we use the equal weighting values $\beta_1 = \beta_2 = 1.0$. Varying these parameters would provide some insight into how the fishery might operate as a result of different points of view but was not done in this study.

Management Policy Performance

Table 2 depicts the performance of the "optimal" management policy with stock risk probability parameter set to both (a) 0.025 and (b) 0.05. The algorithm was run for a 50-yr period (50 overlapping 5-yr planning periods) using temperatures in the Los Angeles Bight from 1933 to 1982. Results are shown for the last 40 yr to remove the effect of the initial condition. This gives a measure of how the fishery would have performed in terms of average yield and of its distribution between the United States and Canadian fisheries had it been operating under this management algorithm over that time period.

For comparison, we show constant effort runs over the same period of (c) 28 000 and 8000 vessel-days for United States and Canadian fisheries, respectively, the MESY effort levels for average sea surface temperature conditions, and of (d) 12 000 and 16 000 vessel-days for United States – Canadian effort combination that gave maximum total average yield over this 40-yr period, considering the actual temperature patterns. Constant effort alternatives were used because they are simple and destabilize stocks less than constant quotas.

The effort combination that gave MESY under average conditions ((c) in Table 2) was far from the best constant effort combination over the 40-yr simulation based on the data (d) (the average of a nonlinear function of a random variable is not equal to the same nonlinear function of the average). The simulation with a risk of 0.025 (a) marginally outperforms the best constant effort case (d) while maintaining a higher minimum stock level. The risk run with 0.05 risk probability (b) gives higher average yield while protecting the stock about as well as the best constant effort case (d). One disadvantage of the risk runs ((a) and (b)) was that the Canadian fishery was shut down for 5 of the 49 yr.

This comparison does not do justice to the policy because it is an a priori policy, while the best constant effort case is chosen a posteriori. To obtain (d) in Table 2, we searched the constant effort space to find the best possible effort combination for the particular temperature data. This was far from the MESY effort levels, which were used as base effort levels for the policy algorithm. Therefore, we cannot assert that the parameters used for the policy algorithm are those that give the highest average yield. On the other hand, searching to find the effort combination (other than MESY effort) that gives the best average yield over the 40-yr temperature data set considered would give results that are too closely tied to this particular data set, while we are more interested in general statements to be made about the effect of using actual data instead of averages of long-term data sets.

Several interesting features with regard to the United States and Canadian yield, respectively,of the risk and constant effort policies are shown in Fig. 5. These features are better observed by considering the temperature data (Fig. 6). The main difference in stock between the two approaches are in the 1950's during a period of cold temperature conditions, where the constant effort stock was significantly lower and in greater jeopardy of collapse, and in the late 1960's when a string of warm years resulted in higher yields and lower stock levels in the risk case. The fluctuating level of yield in the risk runs is also apparent in Fig. 5. One interesting aspect is that the risk policy appears to shut down the Canadian fishery at times when United States effort is highest. This occurs because the United States fishery is responding to a large incoming year class, which only it can harvest, and the Canadian fishery is shut down because its effort will reduce both United States and total yield. This implies that the controlling nature of the United States fishery for hake, which we mentioned earlier in connection with the relative catch in the two fisheries, appears to be strongest with large incoming year classes and an abundant stock. During the period of low stock biomass (the 1950's), however, the Canadian yield remained at a healthy level because of the Canadian effort's focus on older year classes which has less overall effect on the total stock, and allows survival of younger fish.

Multinational Equilibrium Management in a Game Setting

One aspect of multinational management that was only hinted at in the planning horizon work is the interaction between the two fisheries on the same stock. Under the objective of maximizing total yield, we observed times when either one or the other fishery reduced yield to achieve that objective while satisfying the constraints. The nations are usually more competitive.

A framework for examining competitive and cooperative

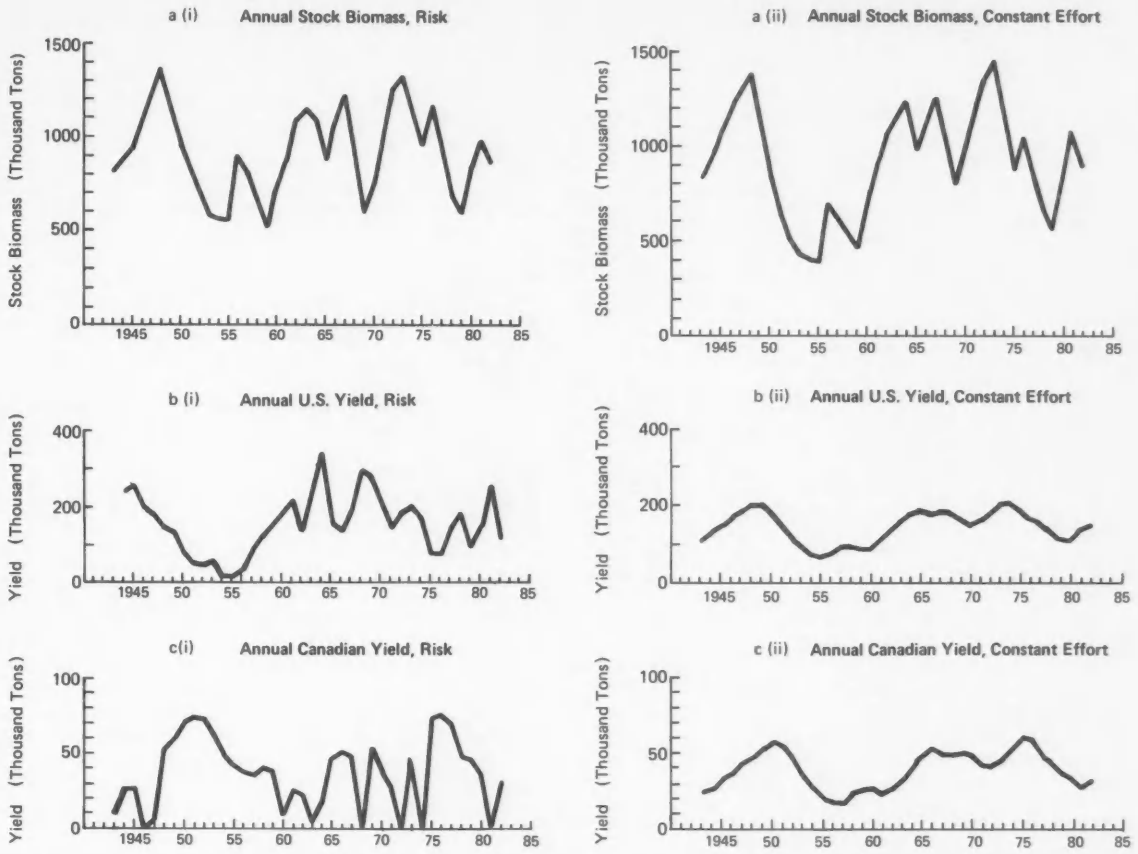
a (i) Annual Stock Biomass, Risk
a (ii) Annual Stock Biomass, Constant Effort
Stock Biomass (Thousand Tons)
b (i) Annual U.S. Yield, Risk
b (ii) Annual U.S. Yield, Constant Effort
Yield (Thousand Tons)
c(i) Annual Canadian Yield, Risk
c (ii) Annual Canadian Yield, Constant Effort
1945 50 55 60 65 70 75 80 85

FIG. 5. Comparison of performance for the optimization algorithm with the constant United States and Canadian effort combinations producing maximum average expected over a 40-yr simulation using temperature conditions in the Los Angeles Bight from 1943 to 1982. Results show annual expected yields for the (a(ii) and a(ii)) Unisted States fishery, (b(i) and b(ii)) Canadian fishery, and (c(i) and c(ii)) total expected stock for the algorithm and constant effort alternatives, respectively.

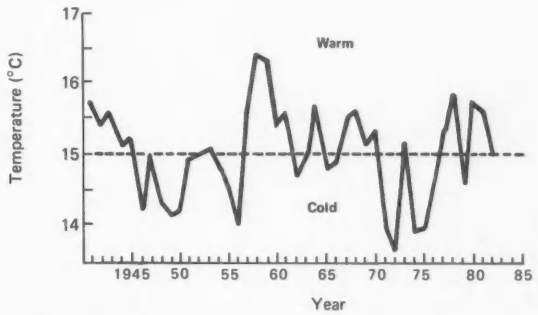

FIG. 6. Temperatures in the Los Angeles Bight from 1943 to 1982 used in the simulations. The broken line separates warm (low or no Eckmann transport) from cold (high Eckmann transport) years.

two-nation management policies is the two-person game. Each "player" is seen as having some strategy — here an effort quota — with the outcome depending on the strategy of each player. To address such a game, we first define the payoff as the average rent over 40 yr from a constant effort harvest policy, where the rent is the income from yield minus the cost associated with the particular effort level. The strategy of each player is to play the same effort each year so as to maximize the average value of the objective function over the last 40 yr of play (1943–82; to eliminate effects due to initial conditions, the first 10 yr are not considered). Here, each player's objective is to maximize his yield minus some weighting factor between 0.0 and 10 times effort. This represents objectives ranging from simply maximizing yield to maximizing a case where fishing effort is costly to the players. Maximizing net profit would fall somewhere within the range of parameters considered. We have not considered games having unbalanced objectives where more weight is given to the yield or more cost to the effort of one country than another, although such games are within the scope of the analysis.

We have chosen this somewhat wide range of objective functions and restricted range of game plays (i.e. no annual, but only long-range game strategies) to allow us to obtain optimal solutions easily and to illustrate the concept of game play in this multinational management setting.

We consider three classes of strategies in this game. The

TABLE 3. Hake equilibria (Nash, maxi−min, and Pareto) for United States − Canada fishery.

Objective function (OF)	Equilibria	v^a	v^c	Y^a	Y^c	Y^{tot}	OF^a	OF^c
Y	Maxi−min	15	16	160	26.5	186.5	160	26.5
	Nash	12	16	156	33.1	189.1	156	33.1
	Pareto	12	16	156	33.1	189.1	156	33.1
$Y - 0.5v$	Maxi−min	15	16	160	26.5	186.5	152.5	18.5
	Nash	15	16	160	26.5	186.5	152.5	18.5
	Pareto	12	12	160	28.8	189	154	22.8
$Y - v$	Maxi−min	14	14	161	26.7	187	147	12.7
	Nash	12	14	158	31	189	146	17
	Pareto	12	2	176	10.2	186	164	8.2
$Y - 2v$	Maxi−min	12	4	171	15.6	187	147	7.6
	Nash	12	6	168	19.8	188	144	7.8
	Pareto	10	4	16	18.9	185	146	10.9
$Y - 5v$	Maxi−min	8	2	160	15.8	176	120	5.8
	Nash	8	2	160	15.8	176	120	5.8
	Pareto	8	2	160	15.8	176	120	5.8
$Y - 10v$	Maxi−min	6	2	145	20.6	166	85	0.6
	Nash	6	2	145	20.6	166	85	0.6
	Pareto	4	2	120	28.4	148	85	0.6

first is called the "maxi−min" strategy and treats the case where each player wants to ensure some average rent but does not know what strategy the other player will play. This is achieved by each player finding his minimum rent for each possible effort quota (assuming the other player will play the strategy that leads to his achieving this minimum) and playing the strategy that leads to the maximum of these minima. Thus, each player is assured of getting at least that value and, if the other player plays a different strategy, to get more.

The second game strategy is called the "Pareto frontier" and is the effort combination (or combinations) that leads to the maximum value of a combined objective function for both players. It is the cooperative case, where one nation may sacrifice individual rent in order to achieve an overall maximum. In combining the rents, we used equal weightings for the individual rents obtained from both players. Other weightings may be chosen, especially when bargaining comes into play (Kaitala 1985; Kaitala et al. 1985; Hamalainen et al. 1984)

The third strategy, the "'Nash equilibrium"' is a case where each player assumes that the other player is rational in a noncooperative setting (Nash 1950). To find this equilibrium point, each player finds the effort strategy that maximizes his objective for each of the other player's strategies. This produces a curve for each player of the locus of all efforts maximizing his rent for all possible strategies of the other player. The intersection of these two curves is the Nash equilibrium. This is an equilibrium of faith in that each player assumes that the other is rational and will play the effort leading to his own maximum rent given that the other player also plays the Nash strategy. Deviation of any player from the strategy would be irrational because they would obtain a reduced rent (even though the reduction to the other player might be greater).

The Nash and maxi−min strategies always give higher efforts, but a lower value of the objective function than the Pareto (Table 3), demonstrating that higher yields can result if both fisheries cooperate. As more weight is placed on the cost of effort in the objective function, the effort levels leading to the optima drop for both fisheries. The drop in effort is initially greatest for the Pareto strategy. As the cost of effort increases in the objective function, relative effort shifts first toward the United States and, when effort cost is high relative to yield income, back toward the Canadian fishery. Average annual yields in the optimal solution remain almost constant with increases in the cost-per-unit-effort relative to the income-per-unit-yield until the cost-per-unit-effort becomes greater than twice the income-per-unit-yield (i.e. the effort coefficient is greater than 2.0). Interestingly, the Nash and maxi−min solutions are very similar for all values of the objective function. The Nash equilibrium, as would be expected, is intermediate between the Pareto and maxi−min strategies (because of the discretization, it is sometimes the same as one or both).

What are the relative advantages of playing a cooperative versus a noncooperative strategy? The Pareto strategy always has efforts for both fisheries less than or equal to the maxi−min or Nash strategy. The Pareto strategy always produces the highest value for the objective function (although not necessarily the highest yield). As effort plays a greater and greater role in the objective function, all strategies result in reduction in effort. Initially these reductions come primarily from the Canadian fishery, but with further increases in effort cost, United States effort becomes substantially reduced. For cases where effort cost is intermediate (e.g. $Y - 0.5v$ and $Y - v$), the United States fishery can achieve a higher rent by playing the Pareto instead of the Nash or maxi−min strategy. For both the cases of maximizing total yield (objective function = Y) and maximizing rent when effort becomes expensive (objective function = $Y - kv$, $k \geq 2$), the United States sacrifices its own rent to achieve a higher total rent. Thus, when the cost of effort is considered in the objectives, it may be to the advantage of either country to play a cooperative strategy, and it is certainly always beneficial to the total fishery. In the real world, changing prices and fuel costs may cause shifts in the profitability of the fishery. Since either fishery stands to gain under some conditions by cooperating, a long-term cooperative management policy, which would tend to reduce effort and stabilize the relative profit for both countries, is the best

strategy for both players.

One striking result from Table 3 is the dramatic drop in Canadian effort in the optimal solution when a weighted function of yield and effort (i.e. rent) is used rather than yield alone as an objective function. This illustrates that little additional yield is obtained when effort in the Canadian fishery is increased in the region of optimal yield. From this perspective it is questionable that fisheries quotas can be set without considering the cost of fishing, but also that fishermen can effectively function within the present management policy based on optimal yield. It seems essential that managers consider the economics of the fishery in a direct way. We realize that the economic analysis of a fishery needed to estimate realistic parameters used in this analysis would be expensive and difficult. Perhaps only error bounds can be placed on the parameters because prices and costs fluctuate. We also recognize that this analysis is oversimplified, but it strongly indicates the value of binational cooperation in managing the fishery and the need for a more detailed study of the implications of a game approach to binational fisheries management. The game approach would be equally useful for cases where two fisheries target on a stock at different stages in its life history. A good example of this is the North Pacific sablefish fishery where the trawl fishery tends to catch primarily younger fish, while the longline fishery targets on larger, older fish. Another example is the United States Pacific coast salmon fishery where a troll fishery targets on the fish in the ocean and a gillnet fishery (primarily native American) targets the returning mature adults.

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Appendix 1. A Stochastic Population Dynamics Model

The hake population is represented here by the mean $\mu_i(t)$ for each age class i at time t and by the covariance $\sigma_{ij}(t)$ between each of the age classes i and j. Originally, we had assumed independence between each of the age classes and used the variance alone to represent variation in the population (Swartzman et al. 1983); however, covariance between age classes can be important, especially after heavy fishing (Horwood 1982).

The stock consists of the fecund stock egg production and is represented by a gamma probability density (Getz 1984). Spawning in this stock occurs before the start of the fishing season — the beginning of the year in our model — and recruitment is assumed to occur at discrete times. The expected recruitment is a function of both stock and the temperature at the time of spawning, with the mean recruitment assumed to be an exponential function of stock (i.e. $R = R_{\max}(1 - e^{-\alpha E})$ for the deterministic case, where E is egg production (Sullivan and Swartzman 1984)), and the coefficient of variation in recruitment assumed to be a constant independent of stock size (but with different values for warm and cold years). With an r-yr lag between spawning and recruitment into the fishery, the recruitment in the youngest age class (age r) in year t is given by (see Getz 1984)

$$(1)\quad \mu_1(t) = R_{\max}(T(t-r)) \times \left[1.0 - \left(\frac{\frac{\mu_e(t)}{\sigma_e^2(t)}}{\frac{\mu_e(t)}{\sigma_e^2(t)} + \alpha(T(t-r))}\right)^{\frac{\mu_e^2(t)}{\sigma_e^2(t)}}\right]$$

where $\mu_1(t)$ = mean recruitment population in year t, $\mu_e(t)$ = mean stock biomass in year t, $T(t)$ = sea surface temperature at the time of spawning in year t, $\sigma_e^2(t)$ = variance in stock biomass in year y, $R_{\max}(T(t))$ = maximum recruitment (different for warm and cold years), and $\alpha(T(t))$ = recruitment parameter (different for warm and cold years).

The variance in the newly recruited age class is represented by $\sigma_{11}(t)$ and is given by (see Getz 1984)

$$(2)\quad \sigma_{11}(t) = (1.0 + cv(T(t-r))^2)R_{\max}(T(t-r))^2 \times \left[1.0 - 2\left(\frac{\frac{\mu_e}{\sigma_e^2}}{\frac{\mu_e}{\sigma_e^2} + \alpha(T(t-r))}\right)^{\frac{\mu_e^2}{\sigma_e^2}} + \left(\frac{\frac{\mu_e}{\sigma_e^2}}{\frac{\mu_e}{\sigma_e^2} + 2\alpha(T(t-r))}\right)^{\frac{\mu_e^2}{\sigma_e^2}}\right] - \mu_e^2(t)$$

where $cv(T(t))$ = coefficient of variation of recruitment (assumed constant over the entire stock range). It depends only on whether sea surface temperature was warm or cold at the time of spawning.

The mean and variance in recruitment are a function of stock and Eckmann transport at the time of spawning — a function that is assumed to not change over time and that is estimated from stock–recruit data on hake (see Swartzman et al. 1983 for details). Covariance between the youngest recruited age class and older age classes is, for general models of this sort, a complex function depending on the stock probability distribution conditioned on the age class population at the time of spawning. For the assumption of a gamma-distributed stock and of an exponential stock–recruit relationship, the following approximation was derived by Sullivan and Swartzman (1984):

$$(3)\quad \sigma_{1j} = [R_{\max}(T(t-r))\mu_j(t) - \mu_1(t)\mu_j(t)]$$

where σ_{1j} = covariance between new recruits and age class j at time t.

Fishing in the model occurs as a constant age and nation-specific fishing rate over a fishing period $\bar{t}$ following the start of the season. Fishing effort in year t (in vessel-days) is distributed between the United States fishery $v_a(t)$ and the Canadian fishery $v_c(t)$. Both the mean and variance in each age class are reduced over the season due to both fishing and natural mortality rates:

$$(4)\quad \mu_{i+1}(t+1) = [\mu_i^a(t)e^{-(m_i+q_i^a v_a(t))\bar{t}} + \mu_i^c(t)e^{-(m_i+q_i^c v_c(t))\bar{t}}]e^{-m_i(1-\bar{t})}$$

where $\bar{t}$ = fishing season (fraction of year), m_i = age-specific natural mortality rate, q_i^a = United States fishery catchability (fishing mortality per unit effort), and q_i^c = Canadian fishery catchability.

The covariance between age classes is updated based on fishing and natural mortality on each of the relevant age classes:

$$(5)\quad \sigma_{i+1,j+1}(t+1) = \sigma_{ij}^a(t)e^{-(m_i+m_j+(q_i^a+q_j^a)v_a(t)\bar{t})} + \sigma_{ij}^c(t)e^{-(m_i+m_j+(q_i^c+q_j^c)v_c(t)\bar{t})}.$$

Notice that for variance updating, $i = j$ and the equation simplifies somewhat. The means and covariances for each age class (μ_i^a, μ_i^c, σ_{ij}^a, and σ_{ij}^c) are distributed between United States and Canadian fisheries such that a constant age-specific fraction of the stock goes to each fishery. Thus, if f_i^a is the fraction of age class i fish going to the United States fishery, then $\mu_i^a = f_i^a\mu_i$ and $\sigma_{ij}^a = f_i^a f_j^a \sigma_{ij}$.

With the above equations we can project the mean and variance of each age class as well as the covariances between age classes forward in time. The stock (egg) mean and variance are computed from the age class means and covariances by

$$(6)\quad \mu_e(t) = \sum_{i=1}^{n} \mu_i(t)c_i e_i$$

$$(7)\quad \sigma_e^2(t) = \sum_{i=1}^{n}\sum_{j=1}^{n} c_i e_i c_j e_j \sigma_{ij}$$

where c_i = proportion of individuals mature in age class i and e_i = egg production per mature age i fish. There is a correction factor (not shown here) for the oldest age class because the model assumes that the recruitment in any year into the oldest age class comes from both itself and from the next-to-oldest age class populations for the previous year.

The mean and variance in yield and in stock are computed from formulae analogous to equations (6) and (7) for the egg mean and variance. The variance terms involve the covariances between age classes just as the egg variance term does.

Appendix 2. The Search Algorithm

The algorithm for finding the quota for United States and Canadian fisheries maximizing the objective function J subject to constraints on stock risk and effort is as follows (Fig. 3).

(1) Divide the United States and Canadian effort levels into discrete sets having units Δv^a and Δv^c, respectively.

(2) Beginning at (0, 0), increase United States effort in steps of Δv^a until either some constraint (stock or effort) is exceeded or the value of J (for that row) begins to diminish. In Fig. 3 the stock constraint is exceeded.

(3) When the constraint or maximum J point is reached in a particular row, the algorithm moves from this point a distance Δv^c and then reduces United States effort in steps of Δv^a until all constraints are satisfied.

(4) The search continues until the United States effort axis is encountered (0 effort) or until the constraint on Canadian effort $v_{\max}^c$ is reached. In each row the maximum J point is saved. These are denoted in Fig. 3 by bold dots.

(5) The "optimal" solution is the maximum value of J from among the row maxima.

The search algorithm uses the fact that if a constraint is violated at one United States – Canadian effort combination, it will certainly be violated when Canadian effort is increased. Although we expect that the optimal solution will be along a constraint boundary, we still check this by reducing effort one unit Δv^a beyond the highest United States effort satisfying all constraints for a given Canadian effort to be sure that the boundary J is the highest in that row.

Although represented in only two dimensions, increase in effort in this algorithm is specified for all h yr of the planning horizon. How this occurs depends on whether effort is above or below the MESY effort levels v^a* for United States effort and v^c* for Canadian effort. Above the MESY effort levels an effort increase of Δv^a in Fig. 3 results in a change in only the first year's effort, while below this level v^a* the increase is in all h yr of effort. The same rule is used for Canadian effort relative to v^c*. This choice of criteria for increasing or reducing effort imposes effort reductions below the MESY level over the entire planning period, while effort increases above MESY occur only in the first year. Thus, strong year classes will be opportunistically exploited, while the loss in yield inherent in a poor stock condition will be spread over the planning horizon.

Because this management algorithm is run over a 50-yr period with the h-yr effort combination chosen each year, the decision in any year affects the decision in the next year through the mean and covariances of the age classes, which are controlled by the fishing effort in the previous year. Thus, the full h-yr "optimal" solution is never implemented, but only the first year effort. The following year's effort will be controlled by the stock condition in the next year, which depends on recruitment in that year and reapplication of the management algorithm.

Microbial Communities on Leaf Material Protected from Macroinvertebrate Grazing in Acidic and Circumneutral Streams[1]

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To determine how low pH and high aluminum concentrations directly affect microbial activity on decomposing leaves in streams, we examined microbial communities on leaf surfaces using in situ flow-through chambers which exclude macroinvertebrates. Bacterial production (thymidine incorporation) on leaf material was significantly higher at pH 6.4 than at 4.9 after 4 wk of incubation, and this difference persisted for the last 5 wk of the experiment. Microbial respiration was greater at the high pH site after 6 wk, and there were no significant differences in ATP standing stock. Concentrations of oxalate-extractable aluminum on the leaf material increased significantly within the first 4 wk of incubation and stabilized at significantly greater levels at low pH (4.66 mg·g^{-1}) than at high pH (1.70 mg·g^{-1}). Transferring leaf material from the high-pH to the low-pH stream had negative effects after only 1 wk of incubation. However, transferring from low pH to high pH did not result in significant positive effects until 4 wk after the transfers. The reduced microbial production and respiration in the low-pH stream imply that decomposition rates may be slower in acidified systems due, at least in part, to direct effects of acidification on microbial activity.

Afin de déterminer la manière dont un faible pH et des concentrations élevées d'aluminium influent directement sur l'activité microbienne ayant lieu sur les feuilles en décomposition accumulées dans des ruisseaux, les auteurs ont étudié des communautés microbiennes présentes à la surface de feuilles gardées dans des compartiments à débit continu *in situ* qui permettent l'exclusion des macroinvertébrés. La production bactérienne (assimilation de la thymidine) sur les feuilles était nettement plus élevée au pH 6,4 qu'au pH 4,9 après 4 sem d'incubation; cette différence s'est maintenue pendant les 5 dernières semaines de l'expérience. Après 6 sem, la respiration microbienne était plus élevée au site à pH élevé et il n'y avait pas de différence significative pour ce qui est du stock de TPA. Les concentrations d'aluminium extractible par oxalate présentes sur les feuilles ont nettement augmenté pendant les 4 premières semaines d'incubation et se sont stabilisées à des teneurs nettement plus élevées à un faible pH (4,66 mg·g^{-1}) qu'à un pH élevé (1,70 mg·g^{-1}). Le transfert de feuilles du ruisseau à pH élevé au ruisseau à faible pH n'a eu une incidence négative qu'après une semaine d'incubation. Toutefois, le transfert d'un faible pH à un pH élevé n'a entraîné des incidences nettement positives qu'après 4 sem. La production et la respiration microbiennes plus basses dans le ruisseau à faible pH montrent que les taux de décomposition peuvent être plus lents dans les systèmes acidifiés à cause, en partie, de l'incidence directe de l'acidification sur l'activité microbienne.

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Although many reports suggest that decomposition of organic matter in surface waters is reduced under acidic conditions (e.g. Friberg et al. 1980; Carpenter et al. 1983; Francis et al. 1984; Burton et al. 1985), decomposition processes in aquatic sediments appear to be relatively insensitive to acidification (e.g. Gahnstrom et al. 1980; Kelly et al. 1984; Hoeniger 1985). Lake sediment pH values are generally much higher than those in acidic surface water as a result of biologically mediated sulfate and nitrate reduction in sediments (Anderson et al. 1978; Wassel and Mills 1983; Kelly et al. 1984); thus, sediment bacteria are living in an environment buffered against acidification. In streams, the pH of the water, and the changes in water chemistry associated with pH or both appear to exert a significant influence on the rate of decomposition of leaf matter. Low pH in streams is frequently accompanied by high aluminum levels. Aluminum is toxic to aquatic organisms (e.g. Baker and Schofield 1982) and may have effects on bacterially mediated decomposition.

The numbers and composition of invertebrate communities are often significantly different at acidic and circumneutral sites in streams (e.g. Friberg et al. 1980). Differences in the activity of shredding macroinvertebrates may contribute to a reduction in measured leaf decomposition rates at low pH (e.g. Hildrew et al. 1984; Kimmel et al. 1985). However, lower rates of microbial activity have also been observed in acidic waters (Carpenter et al. 1983), and reduced microbial decomposition may decrease leaf weight loss rates. Finally, reduced microbial activity at low pH may itself be the result of reduced

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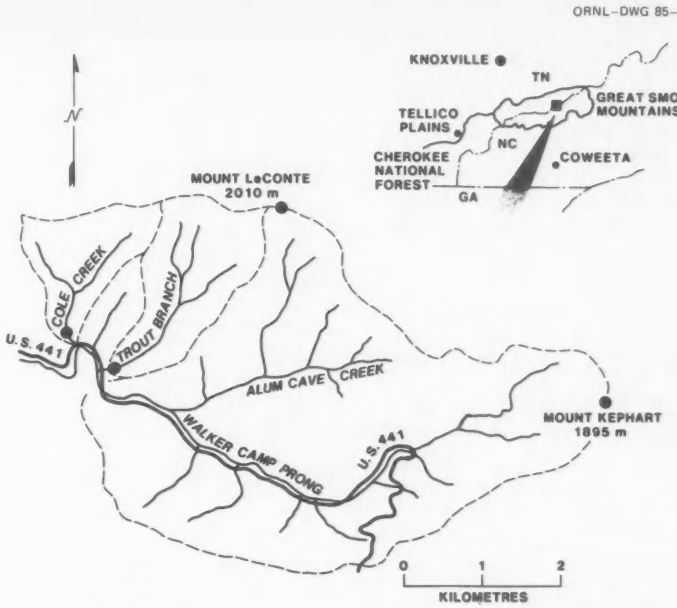

FIG. 1. Walker Camp Prong watershed showing the two streams in this study, Trout Branch and Cole Creek.

invertebrate feeding on the leaf material, thereby reducing the rate of nutrient regeneration and/or increasing the self-limitation of the microbial community due to accumulation of thick layers of cells.

The purpose of this study was to determine if low pH and concomitant elevated aluminum concentrations directly affected the activity of microbes associated with decomposing leaves in streams. We excluded macroinvertebrates and measured indices of microbial biomass (ATP) and activity (tritiated thymidine incorporation into DNA, community respiration) on leaf material at two streams with base flow pH values of 4.9 and 6.4. The effects of acidification and of pH increase on established microbial communities were also examined by exchanging leaf material and the associated microbial community between streams. Because aluminum has been implicated in the toxicity of acidified waters to other organisms, the aluminum levels in the water were measured and aluminum accumulation on the leaf material was followed.

Materials and Methods

Site

The experiments were conducted in Cole Creek (baseflow pH 6.2–6.5) and Trout Branch (baseflow pH 4.9–5.0) in the Great Smoky Mountains National Park (Fig. 1). Both streams are second-order tributaries of Walker Camp Prong and drain the south slope of Mt. LeConte. The two streams are ~1 km apart along Highway 441 and drain unlogged watersheds. The streams in the Walker Camp watershed are acidified to different degrees presumably because of differences in the amount of exposed pyrite-bearing bedrock in the subcatchments. Landslide activity in the higher elevations of the park periodically exposes rocks of the Anakeesta Formation containing pyritic material.

Water Chemistry

Water samples for chemical analysis were taken once a month at each site. Field pH was measured potentiometrically using an Orion (model 221) portable pH meter with an Orion "Ross" glass electrode. Specific conductance and temperature were measured in the field with a portable, digital conductivity–temperature meter with automatic temperature compensation.

Water samples for dissolved organic carbon (DOC) determination were filtered in the field through 0.2-μm Nuclepore filters directly into glass bottles, which were combused at 500°C for 12 h prior to use, containing $HgCl_2$ as a preservative. Samples for phosphorus determination were filtered through a 0.4-μm Nuclepore filter. All samples were then stored at 4°C until analyzed.

Unfiltered samples were analyzed for acid-neutralizing capacity (ANC) by titration with strong acid and Gran plot analysis (Gran 1952) and for NO_3 and SO_4 by ion chromatography (Small et al. 1975). Filtered samples were analyzed for soluble reactive phosphorus (SRP) and total soluble phosphorus (TSP) by the ascorbic acid method before and after persulfate digestion (American Public Health Association et al. 1985). Unfiltered samples for determination of dissolved inorganic carbon (DIC) and filtered samples for DOC were analyzed using an OI Corporation model 700 total carbon analyzer.

Total aluminum (Barnes 1976) and inorganic monomeric aluminum (Driscoll 1984) concentrations in the stream water were measured by atomic absorption spectrophotometry using a graphite furnace. Aluminum associated with the leaf material was extracted using 0.2 *M* ammonium oxalate ($H_2C_2O_4 \cdot 2H_2O_4$ and $(NH_4)_2C_2O_4$) and analyzed using atomic absorption spectrophotometry. Total aluminum associated with the leaf material was not measured.

Experimental Design

Cylindrical plastic chambers (85-mm diameter, 33-mm height) were used for incubating leaf material in the streams. They were constructed to allow water flow but to eliminate macroinvertebrate grazers during incubation. Holes (16-mm diameter) were cut in the top and sides of the chambers and covered with plastic screening (250-μm mesh). Groups of 10 chambers were wrapped together in netting with a large mesh size and staked to the stream bottom in pool areas. Leaf discs (surface area 0.866 cm^2) cut from autumn-shed sugar maple (*Acer saccharum*) leaves with a cork borer were placed in the chambers. The leaves were leached for 24 h and then air dried before being used in the experiments. Twenty-five discs were placed in each chamber.

In June 1985 the chambers were placed in each stream. After 4 wk, five chambers from each site were removed, and microbial respiration, ATP levels, tritiated thymidine incorporation into DNA, and oxalate-extractable aluminum associated with the leaf discs were measured. Half the remaining chambers at each site were transferred to the other stream. Five chambers from each of the four treatments (two original, two transferred treatments) were removed 1 and 5 wk after the transfers (5 and 9 wk after initial placement in the streams, respectively) for the microbial measurements given above. Chambers were also removed at 2 wk after the transfer, but only respiration and amorphous aluminum were measured. A centrifuge failure prevented measurement of tritiated thymidine uptake, and ATP samples were not taken on this date.

Measurements of Microbial Activity and Biomass

Respiration of the microbial community on the leaf discs was measured with a Gilson respirometer at ambient stream water temperatures (Mulholland et al. 1985). On the first sampling date, five leaf discs and 5 mL of stream water were put in each respiration vial. On subsequent sampling dates, nine leaf discs were placed in each vial. At each sampling time, two or three vials per site were run with stream water alone as controls.

ATP levels were measured as an index of microbial biomass. At each sampling time, five leaf discs from each chamber sampled were placed into 5 mL of 1 *M* phosphoric acid and extracted for ATP overnight (Karl and Craven 1980; Palumbo et al. 1987). Subsamples (0.5 mL) of the extract were frozen for later analysis. The 0.5-mL subsamples were thawed and diluted to 20 mL with 0.02 *M* Tris buffer (Palumbo et al. 1987). Subsequent ATP analysis was performed using a Lumac Biocounter with purified Lumac reagents. Internal standardization was used on every sample to calculate ATP concentration.

Tritiated thymidine incorporation into DNA was measured as an indicator of bacterial production on the leaf material. Four or five leaf discs from each chamber were placed in a 50-mL round-bottom centrifuge tube containing 4 mL of water from the site from which the chamber was removed. The tubes were equilibrated to stream temperature, and then 8.31×10^9 Bq of tritiated thymidine (NET-250, New England Nuclear), specific activity 1.04×10^{16} Bq·mmol^{-1}, was added to each tube. The discs were incubated for 20 min, and then 0.5 mL of 37% formaldehyde was added to the tubes. The liquid in the tubes was poured off, and the leaf discs were rinsed with distilled water three times. The extraction of the labeled DNA from the leaf material followed the methods of Findlay et al. (1984). The leaf discs were extracted with 5 mL of 0.3 *M* NaOH, 0.1% SDS, and 25 m*M* EDTA. The solution was neutralized and 5 mL of 10% trichloroacetate and unlabeled DNA was added to the tubes. The tubes were centrifuged at $20\,000 \times g$ for 15 min, and the leaf material and precipitate were collected on Gelman 0.45-μm pore size filters. Collection of the DNA on filters without centrifugation resulted in low recovery of labeled DNA. Five millilitres of 5% TCA was added to the filter and leaf material and extracted for 30 min at 100°C. One-millilitre subsamples of the 5% TCA were counted for radioactivity in a liquid scintillation counter, and external standardization was used to correct to disintegrations per minute. Isotope dilution of the added thymidine by internal or external pools of thymidine was checked during this experiment and during other experiments involving leaf material. At the high levels of added thymidine used in these experiments, we have not detected the dilution of the added thymidine (Palumbo et al., unpubl.).

Results

Differences in water quality exist between the two sites. The pH, ANC, and conductivity were greater in Cole Creek than in Trout Branch (Table 1). The conductivity was higher at Trout Branch but was low at both sites. Note that conductivity and SRP and TSP concentrations were very low at both sites but were slightly higher at Cole Creek. Both total aluminum and inorganic monomeric aluminum were higher at the low-pH site (Trout Branch) than at the high-pH site (Cole Creek), and Ca^{2+} concentrations were only slightly lower at the low-pH site. Nitrate (NO_3) levels are relatively high in both streams. DOC levels in both streams were low (Table 1). We have no data on DOC quality.

Thymidine incorporation into DNA by the bacterial population on the leaf material incubated entirely at high pH, in Cole Creek, was greater ($p < 0.05$) than that on the leaf material incubated at low pH (Table 2), in Trout Branch, on all sampling dates (Fig. 2). Seven days after leaf material was transferred from the high-pH site to the low-pH site, thymidine incorporation into DNA was lower ($p < 0.05$) than that on the leaf material remaining at the high-pH site (Fig. 2). However, the rate of thymidine uptake on the leaf material that was transferred to the high-pH site from the low-pH site was not significantly different ($p < 0.05$) from the rate on the material that remained at the low-pH site. Four weeks later (5 wk after transfer), thymidine incorporation associated with the leaf material transferred from high- to low-pH sites was again significantly lower ($p < 0.05$) than the uptake rate associated with the material remaining at the high-pH site. Also at this time, the leaf material transferred from the low- to high-pH site had significantly greater ($p < 0.05$) thymidine uptake than the samples that remained at the low-pH site. Further, there were significant increases ($p < 0.05$) over time in the rate of thymidine incorporation into DNA on the leaf material incubated in Cole Creek ($r^2 = 0.48$, $N = 12$) and on the leaf material transferred to Cole Creek from the lower pH site ($r^2 = 0.58$, $N = 12$), Trout Branch. There was no significant ($p < 0.05$) trend in the thymidine incorporation over time in the other two treatments.

Although we observed patterns among the treatments in ATP on the leaf discs similar to those for thymidine uptake, no significant differences ($p < 0.05$) in ATP were observed among the treatments at any sampling time (Fig. 2). Also,

TABLE 1. Water quality measurements, including pH, ANC, DOC, DIC, SRP, TSP, and ion concentrations at Trout Branch and Cole Creek. Data presented are mean and standard deviation (SD) of four samples, one each month in May, June, July, and August 1985, at each site.

Variable	Cole Creek		Trout Branch	
	Mean	SD	Mean	SD
pH	6.37	0.04	4.90	0.04
ANC ($\mu eq \cdot L^{-1}$)	16.50	44.3	−16.0	2.3
Temperature (°C)	13.7	1.6	13.5	1.8
Conductivity ($\mu S \cdot cm^{-1}$)	17.6	0.8	21.9	0.6
DOC ($mg \cdot L^{-1}$)	1.14	0.22	0.90	0.33
DIC ($mg \cdot L^{-1}$)	0.67	0.07	0.36	0.02
SRP ($\mu g \cdot L^{-1}$)	1.72	0.20	0.52[a]	0.35
TSP ($\mu g \cdot L^{-1}$)	3.72	1.72	2.32	1.23
SO_4 ($mg \cdot L^{-1}$)	1.87[b]	0.12	4.23	0.19
Ca ($mg \cdot L^{-1}$)	1.48	0.05	1.22	0.05
Total Al[b] ($mg \cdot L^{-1}$)	0.090	0.002	0.17	0.03
Inorganic monomeric Al[b] ($mg \cdot L^{-1}$)	0.003	0.002	0.11	0.03
NO_3[b] ($mg \cdot L^{-1}$)	3.78	0.68	3.18	0.55

[a]Two of the values were below the detection limit of 0.5 $\mu g \cdot L^{-1}$; therefore, a value of 0.25 $\mu g \cdot L^{-1}$ was used for them in calculations of the mean and SD.
[b]Mean of three samples: May, June, and July 1985.

TABLE 2. Analysis of variance for the four sampling dates. The difference between Cole Creek and Trout Branch is listed if it is significant at the 5% level. Week 0 is the time of the transfer and is 4 wk after the leaf material was placed in the streams. Units for the differences between Trout and Cole are 10^{-14} $mol \cdot cm^{-2} \cdot h^{-1}$ for thymidine, $\mu g \cdot cm^{-2}$ for amorphous aluminum, and $\mu mol \cdot cm^{-2} \cdot h^{-1}$ for oxygen uptake. NS = not significant.

Week	Variable	F	$p > F$	df	Difference between Cole and Trout
0	Thymidine	32.52	0.001	1,6	12.68
	Aluminum	20.43	0.004	1,6	−12.81
	Oxygen	1.75	0.234	1,6	NS
	ATP	3.95	0.094	1,6	NS
1	Thymidine	4.72	0.021	3,12	25.05
	Aluminum	6.88	0.006	3,12	−21.35
	Oxygen	1.59	0.249	3,11	NS
	ATP	0.80	0.515	3,12	NS
2	Aluminum	7.45	0.004	3,12	−13.47
	Oxygen	3.56	0.051	3,11	0.198
5	Thymidine	14.39	0.0003	3,12	25.09
	Aluminum	7.98	0.003	3,12	−13.48
	Oxygen	5.32	0.015	3,12	0.095
	ATP	0.68	0.585	3,11	NS

ATP did not increase significantly over time in any of the four treatments (Table 2). The variability of the ATP level on leaf discs at a site was much higher than the variability of thymidine uptake. The mean coefficient of variation for a given treatment at a given time was 48.8% for ATP and 30.4% for thymidine uptake.

Oxygen consumption was significantly greater ($p < 0.05$) 1 and 5 wk after the transfer in the Cole Creek samples than in the samples incubated in Trout Branch (Table 2), or in the samples transferred from Cole Creek to Trout Branch (Fig. 3). At the first sampling period the variability of the oxygen data (mean coefficient of variation of 69.1%) was higher than it was for later sampling periods (mean coefficients of variation of 25.8, 39.2, and 17.8%). The large decrease in the coefficient of variation from the first sampling period to the later periods may be the result of increasing the number of discs in each respiration flask from five to nine. Oxygen uptake exhibited no significant ($p < 0.05$) trends over time in any of the treatments. Thus, although the differences in oxygen uptake among the treatments were similar in pattern to the differences in thymidine uptake, these differences were not significant ($p < 0.05$) until 2 wk after the transplant (Table 2).

The concentration of oxalate-extractable aluminum on the leaf material was higher at all sampling times (Table 1) for the material incubated entirely in Trout Branch (Fig. 3) than for the material incubated entirely in Cole Creek. There was a significant increase in the aluminum concentration at both sites during the initial 4 wk of incubation prior to the transfers. Initial levels of oxalate-extractable aluminum on leaf material were only 0.99 $\mu g \cdot cm^{-2}$. However, by the first sampling time, the aluminum levels had increased to 8.27 and 22.73 $\mu g \cdot cm^{-2}$ at the high- and low-pH sites (Fig. 3). There were no trends in oxalate-extractable aluminum concentration in the samples incubated entirely in Cole Creek or in Trout Branch (Fig. 3) after the initial 4 wk of incubation. There was a significant increase in the aluminum concentration over time ($r^2 = 0.32$, $N = 16$) in the material transferred to Trout Branch from Cole Creek (Fig. 3); however, there was no significant decrease in the aluminum on the leaf material transferred from Trout Branch to Cole Creek (Fig.3).

Thymidine incorporation was positively correlated ($p < 0.05$) with both oxygen uptake ($r = 0.4$, $N = 54$) and ATP ($r = 0.44$, $N = 39$). However, ATP and oxygen uptake were not correlated ($r = 0.23$, $N = 38$). The concentration of oxalate-extractable aluminum was significantly correlated ($p < 0.05$) with both thymidine uptake ($r = -0.28$, $N = 56$) and oxygen uptake ($r = -0.35$, $N = 54$) but not with ATP ($r = -0.01$, $N = 39$).

Due to the small amount of leaf material used and the short length of the experiment (9 wk), there were no detectable

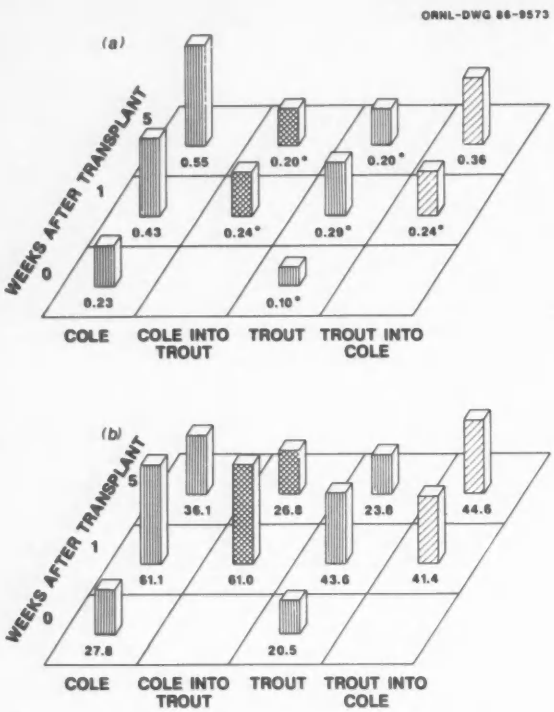

FIG. 2. Microbial response to incubation of leaf material at high and low pH and to transfers between high-pH (Cole Creek) and low-pH (Trout Branch) sites. Differences among treatments were tested for significance (at the 95% confidence level) using analysis of variance on data for each sampling time. Treatments significantly different from that at Cole Creek are indicated by asterisks. (a) Thymidine incorporation into DNA (10^{-14} mol·cm^{-2}·h^{-1}). At week 5, uptake was significantly greater on material transferred from Trout Branch into Cole Creek than on material remaining in Trout. (b) ATP standing stock (ng·cm^{-2}) on leaf material.

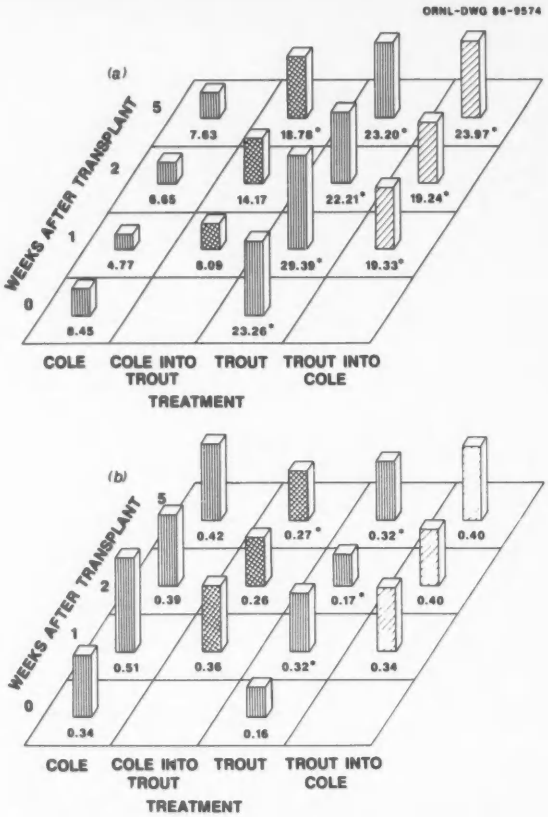

FIG. 3. Oxygen uptake and amorphous aluminum concentration on leaf material at high and low pH and material transferred between high-pH (Cole Creek) and low-pH (Trout Branch) sites. Differences among treatments were tested for significance (at the 95% confidence level) using analysis of variance on data for each sampling time. Treatments significantly different from Cole Creek are indicated by asterisks. (a) Amorphous aluminum concentrations (μg·cm^{-2}). There were significantly greater concentrations at week 5 on material transplanted from Cole Creek into Trout Branch. (b) Oxygen uptake rate (μmol·cm^{-2}·h^{-1}) on leaf material.

changes in dry leaf mass over time. The initial mean dry weight of the individual discs was 4.04 mg (SD = 1.94), and during the experiment the mean dry weight was 4.32 mg. The apparent weight gain is probably due to the accumulation of sediment in the chambers during storms.

Discussion

There were significant differences in the bacterial production and microbial respiration on leaf material between the high- and low-pH sites. Thymidine incorporation into DNA was the most sensitive indicator of reduced microbial activity in response to the differences in water quality. At every sampling period the rate of thymidine incorporation was significantly greater at the high-pH site than at the low-pH site. Oxygen uptake also responded to the differences in water quality but the differences were significant only after a longer incubation period in the stream (Fig. 2 and 3). ATP, a measure of biomass, was not a sensitive indicator of the response of the microbial community to changes in water chemistry. At no time during the study did ATP data indicate that there were significant differences among the treatments (Table 1).

These results are consistent with other studies in which measures of bacterial activity have been shown to be more sensitive indicators of microbial responses to acidification than have biomass measures. For example, Carpenter et al. (1983) found that the decomposition rate of leaves was slower at reduced pH and that the heterotrophic uptake of glucose by the bacteria associated with the leaf material was also depressed at reduced pH. However, no significant differences were observed by Carpenter et al. (1983) in the number of bacteria on the leaves among the sites. Reductions in epilithic community respiration after exposure to acidic conditions have been reported for experimental stream systems (Allard and Moreau 1985). Further, in studies of water column bacteria, numbers appear to be relatively insensitive to acidification effects (e.g. Traaen 1980; Boylen et al. 1983; Rao and Dutka 1983) whereas respiration, substrate utilization, and the number of respiring bacteria are reduced under acidic conditions (Traaen 1980; Rao and Dutka 1983; Rao et al. 1984).

The results of our study indicate that microbial activity associated with decomposing leaves is affected by low pH conditions in the absence of macroinvertebrates. The negative correlations between oxalate-extractable aluminum and thymidine and oxygen uptake implicate aluminum as a factor in this reduction in microbial activity at low pH. However, the relationship between elevated aluminum concentrations and reductions in microbial activity has not been clearly demonstrated, and this study does not conclusively make the link. Aluminum does appear to have a significant role in the toxicity of acidified waters to fish (e.g. Driscoll et al. 1980; Schofield and Trojnar 1980; Muniz and Leivestad 1980; Baker and Schofield 1982). In one of the few studies where microbial activity was not reduced under acidic conditions (Hoeniger 1985), the lowest pH lake tested varied seasonally in pH between 5.6 and 5.8. At those pH levels the concentration of inorganic monomeric aluminum in the water should still be very low (e.g. Stumm and Morgan 1981), and the lack of a significant effect may be related to the comparatively high pH and low aluminum levels. In the present study, lower rates of bacterial production and respiration at the low-pH, high-aluminum site were accompanied by significantly greater accumulations of oxalate-extractable aluminum on the leaf material and associated bacteria (Fig. 2 and 3). As pointed out by Hall et al. (1985), aluminum occupies surface adsorption sites on cell and tissue surfaces and may interfere with ion exchange mechanisms (Muniz and Leivestad 1980). Thus, the bacteria on the leaf material would be subject to adsorption of aluminum and potential physiological interference.

The mechanism for the oxalate-extractable aluminum accumulation could be either adsorption or precipitation, or both. The patterns of accumulation implicate adsorption of aluminum on the leaf and bacterial surfaces as the mechanism for aluminum accumulation. The surfaces of detritus particles characteristically have a strong negative charge (Stumm and Morgan 1981). Thus, adding fresh detritus to a stream system should result in adsorption of positively charged aluminum on the leaf surfaces. The level of oxalate-extractable aluminum on the leaf surfaces increases within the initial 4-wk incubation period from low initial levels, 0.996 $\mu g \cdot cm^{-2}$ (~0.21 mg Al·g leaf material^{-1}), to levels of 8.27 $\mu g \cdot cm^{-2}$ (~1.70 $mg \cdot g^{-1}$) and 22.7 $\mu g \cdot cm^{-2}$ (~4.66 $\mu g \cdot g^{-1}$), respectively, in the high-pH and low-pH streams. No additional accumulation took place in the next 5 wk, suggesting that an equilibrium was reached in the first 4 wk. The leaf material transferred from the high-pH stream to the low-pH stream exhibited an increasing concentration of oxalate-extractable aluminum after the transfer; however, most of the increase occurred within the first 2 wk after transfer (Fig. 3). The apparent equilibria reached in each stream suggest an adsorption process rather than precipitation, since aluminum concentration would probably continue to increase if precipitation were occurring. However, the equilibration of particle surfaces with added inorganic aluminum is a very rapid process, on the order of minutes (Hall et al. 1985) rather than weeks. Thus, precipitation reactions may also contribute to the accumulation of oxalate-extractable aluminum on the leaf material.

The differences in microbial activity between the streams are potentially related to differences in pH, aluminum, and phosphorus concentrations. Phosphorus levels in the low-pH stream tended to be lower than in the high-pH stream (Table 1), perhaps due to coprecipitation with aluminum. Phosphorus concentrations were very low at both sites (Table 1), and the molar ratios of nitrogen to phosphorus were very high, >1000:1. Thus, these streams are potentially phosphorus limited (Elwood et al. 1981). However, leaf decomposition studies we conducted subsequent to this study indicated that reduced microbial activity at low pH was not primarily a result of greater phosphorus limitation at low pH (Mulholland et al., unpubl.). Therefore, we conclude that microbial activity associated with decomposing leaves in streams is reduced at pH values of 4.9 compared with pH values >6 and that the apparent inhibition may be related to aluminum interferences.

We have no information on the levels of protozoans or fungi on the leaf material at the two sites. Differences in protozoan grazing could contribute to the differences observed in this study, and we would expect that the importance of fungi in the decomposition would increase under acidic conditions, especially since the rate of bacterial production in the lower pH stream is reduced.

Differences in concentrations of other metals, the sediment loads, and the algal production in the two streams probably do not contribute to the difference in bacterial production. Trace metal data indicate that only aluminum and manganese at the Cole Creek are elevated over levels at Trout Branch (Mulholland et al. 1986, table 1). Concentrations of other trace metals such as mercury, cadmium, lead, copper, and zinc were undetectable. Sediment loads at base flow in the two streams are comparable, 0.267 $mg \cdot L^{-1}$ ($N = 5$) in Cole Creek and 0.276 $mg \cdot L^{-1}$ ($N = 5$) in Trout Branch (unpubl. data). Algal biomass and production is actually greater at the low-pH site (Mulholland et al. 1986).

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NOTES

Infectious Hematopoietic Necrosis Virus Detected by Separation and Incubation of Cells from Salmonid Cavity Fluid

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Mulcahy, D., and W. N. Batts. 1987. Infectious hematopoietic necrosis virus detected by separation and incubation of cells from salmonid cavity fluid. Can. J. Fish. Aquat. Sci. 44: 1071–1075.

Infectious hematopoietic necrosis (IHN) virus is usually detected by inoculating susceptible cell cultures with cavity ("ovarian") fluid (CF) from spawning females. We identified additional adult carriers of virus in spawning populations of steelhead trout (*Salmo gairdneri*) and sockeye salmon (*Oncorhynchus nerka*) by collecting nonerythrocytic cells from CF samples by low-speed centrifugation, culturing the cells for at least 7 d at 15°C, and then testing the culture medium for virus. Virus appeared in the cultured cells from some samples of CF that remained negative during incubation. In additional samples of CF from these species, the virus titer increased in cultured cells compared with the titer in the original CF sample. With chinook salmon (*O. tshawytscha*), no negative samples converted to positive during incubation, but the virus titer was retained in incubated CF cells, but not in cell-free CF.

En général, on révèle la présence du virus de la nécrose hématopoiétique infectieuse (NHI) par inoculation de cultures de cellules sensibles avec du fluide corporel (« ovarien ») de femelles génitrices. Les auteurs ont identifié d'autres adultes porteurs du virus chez des populations génitrices de truites arc-en-ciel (*Salmo gairdneri*) et de saumon nerka (*Oncorhynchus nerka*) en recueillant des cellules autres que des érythrocytes dans les échantillons de fluide corporel par centrifugation à basse vitesse. Les cellules ainsi obtenues ont été cultivées pendant au moins 7 j à 15°C; le milieu de culture a ensuite été testé pour la mise en évidence du virus. Celui-ce est apparu dans les cellules cultivées de certains échantillons de fluide corporel qui sont demeurés négatifs pendant l'incubation. Chez des échantillons supplémentaires de fluide corporel obtenu de ces espèces, le titre du virus a augmenté dans les cellules cultivées par rapport au titre de l'échantillon original de fluide corporel. Chez le saumon quinnat (*O. tshawytscha*), aucun échantillon négatif n'a montré une réaction positive pendant l'incubation, mais le titre du virus a été retenu dans les cellules incubées de fluide corporel mais non dans le fluide corporel libre de cellules.

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Infectious hematopoietic necrosis (IHN) virus is usually detected in spawning female salmonid fishes by inoculating susceptible cell cultures with cavity ("ovarian") fluid (CF) obtained at spawning. La Patra and Groberg (1985) reported the appearance of IHN virus in eggs and CF of steelhead trout (*Salmo gairdneri*) held for delayed fertilization in plastic bags under oxygen for 8 d at 4°C, although no virus was detected in samples of CF taken at the time of spawning. They did not discuss a possible mechanism for the spontaneous appearance of IHN virus in the stored eggs and fluid.

In this report, we show that this phenomenon occurs in CF samples stored without the presence of eggs, that it can be demonstrated by using CF from sockeye salmon (*Oncorhynchus nerka*) and possibly chinook salmon (*O. tshawytscha*), as well as steelhead trout, and that the probable source of virus is de novo synthesis by cells present in the CF.

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Materials and Methods

For virus detection and quantification, we used the plaque assay of Burke and Mulcahy (1980) as modified by Mulcahy et al. (1982). The cell culture medium used and the taking and processing of spleen and CF samples at spawning were described by Mulcahy et al. (1982).

Steelhead trout — We used CF collected in January, February, and March 1985 from steelhead trout at Round Butte Hatchery (Portland General Electric and Oregon Department of Fish and Wildlife) in Oregon for three experiments. In the first, we put 0.5–8 mL of CF from each of 50 fish into individual 25-cm^2 cell culture flasks and added an equal volume of minimum essential medium with 10% fetal bovine serum (MEM-10). The undiluted CF and the diluted CF from each flask were tested for virus. The CF was then held at 4°C and the flasks were incubated at 15°C for 10 d and then both were retested for IHN virus.

TABLE 1. The IHN virus titers (log_{10} pfu/g or pfu/mL) in the 7 of 61 fish in the second steelhead trout experiment that converted from negative to positive. Spleen and CF samples were taken at the egg take (first sample) and CF was taken from the stored eggs 8 d later (second sample). Samples of CF and cultured cells were incubated for 9 d (first sample) or 7 d (second sample).

Fish No.	At egg take		At fertilization	After incubation			
				First sample (9d)		Second sample (7d)	
	Spleen	CF	CF	CF	Cells	CF	Cells
13	0	0	2.04	0	0	0	0
24	0	0	1.54	1.18	1.60	0	3.72
28	1.70	0	1.54	0	0	0	0
40	0	0	0.70	0	0	0	6.51
57	0	0	2.20	1.18	0	0	0
60	0	0	1.18	0	0	0	3.04
1	0	0	0	0	3.90	0	0

The second and third steelhead trout experiments were parts of delayed fertilization projects in which eggs and CF from individual females were stored under oxygen at 4°C for 9 d before fertilization. Samples of spleen and CF were taken from 61 fish in the second experiment and from 118 fish in the third experiment and processed for virus isolation within 24 h. Cells were separated from CF by centrifugation (50 × *g*) and the cell-free CF was carefully removed. The cells were resuspended in 1 mL of MEM-10 and placed into a single well of a 24-well cell culture plate (Linbro 76-033-05); the plates and cell-free CF were then incubated for 9 d (second experiment) or 7 d (third experiment) at 15°C, after which the cultures and samples were retested for IHN virus. On the same day that the samples were retested, the eggs were removed from storage and an additional sample of CF was taken prior to fertilization. The cells and CF were separated as above and incubated at 15°C for 7 d before retesting.

Spring chinook salmon — A total of 84 CF samples of various volumes (>5 mL) were collected in September 1985 from spawning spring chinook salmon at Leavenworth National Fish Hatchery (U.S. Fish and Wildlife Service). The samples were tested for IHN virus within 24 h. The cells and CF were separated as above and incubated for 7 d at 15°C before retesting.

Sockeye salmon — We took CF samples from 52 ripe and 45 spent sockeye salmon collected in October and November 1985 from the Cedar River, Washington. The incidence of IHN virus in this population has always exceeded 95% (Mulcahy et al. 1982, 1984a). The experimental design was identical to that described above for spring chinook salmon, except that in one experiment with ripe fish, we tested some of the cultured cells twice: after 7 and 14 d of incubation.

Results

In the first steelhead trout experiment, the cells were not separated from the CF sample prior to incubation. The initial IHN virus infection rates for the fish, as determined by immediate testing, were 32% using the CF and 26% using the cultured cells. After 10 d of storage, one negative CF sample became positive (5 plaque-forming units (pfu)/mL); no virus was isolated from the cultured cells from this sample. After 7 d of incubation, the infection rates were 30% using the CF and 22% using the cultured cells. The overall infection rate (considering the results from the original CF, the incubated CF, and the cultured cells) was 34%. In one fish, the virus titer on the first day was 1.87 log_{10} pfu/mL in the undiluted CF and 1.48 log_{10} pfu/mL in the diluted CF taken from the flask. After 10 d of incubation, the titers for that fish were 0.70 log_{10} pfu/mL in CF and 6.11 log_{10} pfu/mL in the cultured cells in the flask, indicating that IHN virus replication in CF cells was the source of the increased virus concentration previously seen in stored CF samples.

TABLE 2. IHN virus titers (log_{10} pfu/g or pfu/mL) for fish that yielded CF samples that converted from negative to positive in the third steelhead trout experiment with 118 fish. Spleen and CF samples were taken at the time the eggs were taken (first sample) and CF was taken from the stored eggs 8 d later (second sample). Cont. = contaminated.

Fish No.	At egg take		At fertilization	After incubation (7 d)			
				First sample		Second sample	
	Spleen	CF	CF	CF	Cells	CF	Cells
21	0	0	1.00	0	Cont.	0	2.28
33	0	0	1.18	0.70	Cont.	0	1.18
42	0	0	0.70	0	0	0	0
47	0	0	0.70	0	0	0.70	3.00
49	2.65	0	1.20	1.00	0	0.70	0
62	0	0	0.70	0.70	0.70	0.70	1.00
70	0.70	0	0.70	0	1.00	0.70	0
71	0	0	1.18	1.40	0	0	0
103	0	0	0.70	Cont.	0	0	0
104	2.65	0	1.00	Cont.	0	0	0
107	0	0	0.70	Cont.	0	0	2.28
109	0	0	2.89	Cont.	0	2.85	3.70
111	0	0	2.54	Cont.	2.71	2.15	2.96
117	0	0	1.30	Cont.	3.51	1.18	2.45
38	0	0	0	0	0	0	1.90
43	0	0	0	0.70	0	0	0

In the second steelhead trout experiment, infection rates at the time the eggs were taken from 61 fish were 18% using spleen samples and 31% using CF samples. Of the 42 fish with initially negative CF, 6 (14%) converted to positive at the time the eggs were removed from storage, bringing the infection rate to 36% (Table 1). The highest virus titer in the converted samples was 2.20 log_{10} pfu/mL; virus was initially present in the spleen of only one of these fish. Sizable increases (up to 2 log_{10} pfu/mL) in virus titer from that in the initially positive CF sample to that in the CF taken from the eggs when they were removed from storage occurred in several other fish (data not shown). Incubation of CF and cultured cells caused a considerable loss of virus. The infection rates in the first CF sample dropped to 18% in the incubated CF and 21% in the CF cells after 7 d. After incubation of the second sample of CF, obtained at the time the eggs were removed from storage, the infection rate in the CF was reduced to 8%, but 25% of the cultured cells were virus-positive. Considering all types of samples, the overall infection rate was 43% for the 61 fish in this experiment. For fish No. 40 (Table 1), the only positive samples were the CF taken from the stored eggs at fertilization (5 pfu/mL) and the second sample of cultured cells in which an extremely high titer (6.51 log_{10} pfu/mL) had developed.

TABLE 3. IHN virus titers (log_{10} pfu/mL) obtained from CF samples from 52 ripe sockeye salmon and from CF and CF cells incubated at 15°C for 7 or 14 d. Results are shown only for fish that had negative initial CF samples and positive incubated CF or CF cells and for examples of fish with initially positive CF samples and poor persistence of virus in CF after 7 d. ND = not done.

Fish No.	CF	After 7 d		After 14 d
		CF	Cells	Cells
2	0	0	0	1.18
8	0	0	1.48	0
13	0	0	6.78	4.98
14	0	0	1.18	0
17	0	0	5.64	5.51
76	0	0	5.45	ND
93	0	1.40	0	ND
4	1.54	0	4.11	3.41
20	2.46	0	5.45	4.38
70	1.30	0	6.79	ND
1	2.43	1.00	5.83	5.20
62	2.81	1.18	5.70	ND
65	2.34	1.00	6.61	ND
88	3.18	1.85	5.51	ND
90	2.60	1.18	6.28	ND
94	1.00	1.18	5.73	ND
97	3.83	2.92	5.88	ND

Fish No. 60 showed a similar pattern. Fish No. 1 was noteworthy because only the first sample of cultured cells was positive (3.90 log_{10} pfu/mL); virus was never detected in a cell-free CF sample from this fish. Three fish, two of which had low levels of virus, reverted from positive on the initial sampling of CF to negative at fertilization (data not shown). One of these, with an initial titer of 3.11 log_{10} pfu/mL, produced virus (3.87 log_{10} pfu/mL) in cells cultured from the first CF sample; all other samples were negative.

In the third steelhead trout experiment, infection rates in 118 fish, tested on the day the eggs were taken, were 31% for spleens and 79% for CF (Table 2). After 8 d of storage, IHN virus was detected in CF samples from 14 fish that had been negative at first sampling, increasing the infection rate to 91%. Again, spleen testing was not useful in predicting the conversion. However, for a few fish that had very low levels of virus appearing in the CF sampled at fertilization, no virus was detected in the equivalent incubated CF or cells. Incubation of CF and cells from the sample taken when the eggs were collected did not account for as many of the conversions from negative to positive in the stored eggs as did the results obtained from incubation of CF and cells from a sample taken at the time the stored eggs were removed from storage and fertilized. The infection rates given by the incubation of CF and cells from the sample taken when the eggs were collected were 68% for the incubated CF and 61% for the incubated cells. The infection rates given by the samples collected when the eggs were fertilized were 61% for the incubated CF and 62% for the incubated cells. As with the previous experiment, several fish that were initially positive had increased titers of virus in subsequent samples, particularly in the incubated CF cells (data not shown). A total of 11 fish in this experiment reverted from positive first CF samples (with low levels of virus ranging from 5 to 20 pfu/mL) to negative CF at the time of fertilization. Virus was isolated from incubated first or second CF samples and cells from seven of these, at levels of up to 2.45 log_{10} pfu/mL.

TABLE 4. IHN titers (log_{10} pfu/mL) of CF samples from 45 spent sockeye salmon and of CF and CF cells incubated at 15°C for 7 d. Results are shown only for fish that had negative initial CF samples and positive CF or CF cells and for examples of fish with initially positive CF samples but with poor persistence of virus in CF after 7 d.

Fish No.	CF	After 7 d	
		CF	Cells
413	0	0	4.57
505	0	0	4.18
407	0.70	0	5.40
500	6.23	0	4.62
501	1.60	0	4.60
606	2.73	0	2.41
617	2.68	0	4.20
620	3.26	0	2.95
621	5.45	0	3.90
622	3.97	0	3.48
625	7.18	0	6.08
626	1.40	0	5.68
402	3.81	2.38	4.76
410	1.00	0.70	5.46
802	0.70	0.70	1.95
803	3.59	3.15	4.76

Spring chinook salmon — The initial IHN virus infection rate in the 84 CF samples taken from spawning spring chinook salmon was 55%. After incubation of the CF samples and cultured CF cells, none of the negative samples converted to positive. A total of 17 CF samples reverted from positive to negative after incubation; the highest initial titer in these samples was 2.79 log_{10} pfu/mL (data not shown). The virus titers in the cultured cells from five fish remained at or near the level found in the original CF, but the titers in the corresponding incubated CF samples decreased, suggesting viral replication in the cultured cells.

Sockeye salmon — The IHN virus infection rate in the initial CF sample from 52 ripe sockeye salmon sampled was 58% (Table 3). Six fish converted from negative to positive after incubation of CF or CF cells for 7 d at 15°C; one additional fish (No. 2, Table 3) produced virus in the cultured cells after incubation for 14 d, but not after 7 d. One of the seven fish that converted from negative to positive had virus in the incubated CF but not in the cells. After incubation, the infection rate was 42% by CF and 56% by CF cells. All of the fish with initially positive CF showed significant increases in virus titer in the cultured cells but not in the incubated CF (Table 3). A total of six initially positive CF samples (all with titers of less than 2.70 log_{10} pfu/mL) were negative in both the CF and cultured cells after incubation (data not shown). Considering all samples, the overall infection rate in the ripe sockeye salmon was 71%.

The IHN virus infection rate in the initial CF sample from the 45 spent sockeye salmon was 80%. After incubation for 7 d, the infection rates were 51% in CF and 76% in the cultured cells. Two fish converted from negative to positive after culture of the cells; virus was not present in the incubated CF (Table 4). Virus could not be isolated from the incubated CF of 10 fish, including 2 with initial virus titers exceeding 6.00 log_{10} pfu/mL; virus titers in the cultured cells from these fish

generally remained high and in some cases increased from the original CF titer (Table 4). Again, several fish with originally positive CF samples showed substantial increases in titer in the cultured cells that were not evident in incubated CF (Table 4). Considering all samples, the overall infection rate in the spent sockeye salmon was 84%.

Morphology of cultured cells — It was not possible to standardize the amount of CF taken from each fish because of the different volume each produced. We collected from 0.5 to 15 mL of CF from a paper cup containing about 60 cm^3 of eggs and fluid from each fish. Comparisons of the relative sizes of the white-colored cell pellets obtained by centrifugation of CF samples of similar volumes from different fish showed that there were differences in the concentrations of cells present in CF. The morphology of the cells was examined after the pellet was resuspended in cell culture growth medium and placed in a well of a cell culture plate. Most of the cells were adherent and were present singly or in small clumps. Masses of up to hundreds of epitheloid, ciliated cells were sometimes seen moving through the medium or attached to the plate. Frequently in such masses, ciliar movement could be observed for the duration of the incubation period. Most of the adherent single cells appeared to be macrophages and lymphocytes, as judged by staining and morphologic criteria (W. T. Yasutake, National Fishery Research Center, Bldg. 204, Naval Station, Seattle, WA 98115, USA, pers. comm.). Many of the cells multiplied to form colonies. If IHN virus was present, the cells underwent typical changes associated with IHN virus cytopathic effects. In several cultures, some cells survived the presence of the virus, and may have been persistently infected with IHN virus.

Discussion

La Patra and Groberg (1985) described the conversion of steelhead trout CF from IHN virus-negative to virus-positive after storage of ova and CF at 4°C for 8 d. We determined that this phenomenon did not require the presence of ova, as it occurred in CF alone and that the conversion occurred in sockeye salmon as well as in steelhead trout. No conversion from negative to positive was seen in CF from chinook salmon. However, chinook salmon CF cells, but not CF, retained the original virus titer after incubation for 7 d. With further work, it is likely that the conversion phenomenon will be demonstrated in this species.

The source of the virus appearing in stored samples was probably the cells present in the CF because the conversion could be demonstrated in some CF samples by culturing the CF cells, but not by holding cell-free CF under identical conditions. The maximum virus titer attained in cultured cells taken from a previously negative CF sample was the same (about 6.00 $\log_{10}$ pfu/mL) for both steelhead trout and sockeye salmon. In addition to conversion of samples from negative to positive, the virus titer increased substantially in the cultured cells, but not in the cell-free CF, from some initially positive CF samples.

The cell population present in CF was heterogenous, consisting of large numbers of epithelial cells and leukocytes. Although we did not identify the specific type of cell responsible for production of IHN virus, macrophages and lymphocytes were considered the most likely candidates because of their involvement in the latency and persistence of viruses in other hosts (Mims 1974; Narayan et al. 1983; Murphy 1978; Montplaisir and Martineau 1978). Knowledge of salmonid leukocytes has increased in recent years (Ellis 1977), and methods for the isolation and in vitro study of salmonid macrophages have been developed (Braun-Nesje et al. 1981, 1982). These developments should make it possible to classify CF cells and to determine the involvement of specific subpopulations of CF cells in the spontaneous appearance of IHN virus in stored samples of salmonid CF.

In some fish used in delayed fertilization experiments, a CF sample taken after storage of the ova for 7 d converted to virus-positive, but the cultured cells from the original CF sample remained virus-negative. In these animals, too little CF may have been collected, containing too few cells to initiate detectable virus production. The larger volume of CF and cells remaining with the ova would have contained enough cells for those with IHN virus to begin producing virus, causing secondary infection of the other cells present. Although we did not study the kinetics of the production of IHN virus in cultured CF cells, we tested certain samples after 14 d, as well as 7 d, of incubation. Some of these required the extra incubation time to produce IHN virus, indicating that a longer incubation time than we routinely used would reveal the conversion of more samples. Virus replication in CF samples probably occurs continuously. This conclusion is supported by the delayed fertilization experiments with steelhead trout, in which two samples of CF were taken, one when the eggs were collected for storage and one 8 d later, at the time of fertilization. In at least one fish (fish No. 38, Table 2), IHN virus was found only in the cells cultured from the second CF sample. In other samples, the virus titer increased in the second sample of cultured cells relative to that present in CF taken at the time of fertilization.

The phenomenon described by La Patra and Groberg (1985) and investigated in our study should be of concern to virologists testing fish. However, the conversion of CF samples from negative to positive upon storage occurred in only a small proportion of CF samples tested, and only when there was an abundance of other, easily detected positive samples. Therefore, it is highly likely that the virus would be found in at least some samples from a population of ripe fish, without the use of the conversion phenomenon. The presence in inocula of CF may explain the occasional very late appearance of cytopathic effect that has been seen in some inoculated cell cultures (data not shown) and the occurrence of small plaques seen in the plaque assay for IHN virus (Mulcahy et al. 1984b).

The putative lifelong, latent carrier state of IHN virus in salmonid fishes has never been directly demonstrated. Evidence for it consists of the appearance of the virus after the sexual maturation of survivors of an epizootic, and the sudden appearance of the virus in Pacific salmon returning to spawn (Amend 1975; Mulcahy et al. 1984a). The CF cells responsible for the production of virus in this study may be the site of latent IHN virus during the prespawning years of life.

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Testing of Male Sockeye Salmon (*Oncorhynchus nerka*) and Steelhead Trout (*Salmo gairdneri*) for Infectious Hematopoietic Necrosis Virus

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Infectious hematopoietic necrosis (IHN) virus has been isolated only rarely from whole milt samples of male sockeye salmon (*Oncorhynchus nerka*). In 3 yr of testing, virus incidences in males ranged from 0 to 13% when milt was sampled but were 60–100% with spleen or kidney. When IHN virus was isolated from sockeye salmon milt at titers less than 3.00 $\log_{10}$ plaque-forming units (pfu)/mL, the level of virus in the kidney or spleen exceeded 7.00 $\log_{10}$ pfu/g. Higher rates of IHN virus isolation from kidney or spleen than from milt were also generally found in steelhead trout (*Salmo gairdneri*), although the differences were less pronounced than in sockeye salmon. Furthermore, virus was sometimes isolated from steelhead trout milt when the level of virus in kidney or spleen samples was very low, and was recovered from some milt samples when none was isolated from the corresponding spleen sample. When male salmonids are tested for IHN virus, kidney or spleen samples are superior to whole milt, but milt should be included for critical examinations.

Le virus de la nécrose hématopoiétique infectieuse (NHI) n'a été que rarement isolé d'échantillons de laitance entière de saumon nerka (*Oncorhynchus nerka*) mâle. En 3 années de vérifications, la présence du virus chez les mâles a varié de 0 à 13 % dans les échantillons de laitance mais a atteint de 60 à 100 % dans les échantillons de rate ou de reins. Quand le virus de la NHI a été isolé de la laitance du saumon nerka à des titres inférieurs 3,00 $\log_{10}$ unités de formation de plaques (pfu)/mL, la concentration du virus dans les reins ou la rate dépassait 7,00 $\log_{10}$ pfu/g. En général, on a aussi obtenu des taux plus élevés d'isolation du virus de la NHI des reins ou de la rate que de la laitance chez la truite arc-en-ciel (*Salmo gairdneri*), mais ces différences étaient moins prononcées que chez le saumon nerka. De plus, on a parfois pu isoler le virus de la laitance de la truite arc-en-ciel quand la teneur en virus des échantillons de reins ou de rate était très faible; on a aussi découvert le virus dans certains

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échantillons de laitance quand aucun n'avait été isolé dans l'échantillon de rate correspondant. Les échantillons de reins ou de rate sont supérieurs à la laitance entière pour le dépistage du virus de la NHI chez les salmonidés mâles, mais la laitance devrait être incluse pour des examens critiques.

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The inspection and certification of brood stock salmonids for viruses is the cornerstone for the control of these pathogens. Milt samples formerly were acceptable for the examination of spawning fish, especially rainbow trout (*Salmo gairdneri*), for viruses. The recently revised protocols now emphasize the use of cavity ("ovarian") fluid (CF) samples (Department of Fisheries and Oceans 1984; Amos 1985). The suitability of milt as a sample (relative to visceral samples) for the detection of infectious hematopoietic necrosis (IHN) virus has not been evaluated.

The use of milt for testing male salmonid fishes for IHN virus was adopted by extrapolation from the use of CF samples for testing females, rather than by empirical methods. Similarly, the present trend away from the use of milt samples is based on anecdotal evidence of its lack of usefulness. The IHN virus incidences in populations of male sockeye salmon (*Oncorhynchus nerka*) tested by sampling milt were much lower than the incidences obtained by testing CF from females of the same populations (Grischkowsky and Amend 1976). Differences in virus incidence were also reported for male and female chinook salmon (*O. tshawytscha*) (Wingfield and Chan 1970). However, Amend (1975) found no difference in the incidence of IHN virus between genders of rainbow trout, and his work was responsible for the acceptance of milt samples for examination of spawning rainbow trout populations (McDaniel 1979).

We compared the incidence and titer of IHN virus in milt samples with those in kidney and spleen samples from spawning male sockeye salmon and steelhead trout (*S. gairdneri*). For both species, testing kidney or spleen was usually superior to whole milt for the detection of IHN virus. For critical examinations of brood stocks, however, milt samples should be used as well as visceral organs.

Materials and Methods

Male sockeye salmon spawning in the 1980 brood year in the Cedar River, Washington, were tested by examining seven visceral organs and serum and milt. In the 1982 brood year, 12 male Cedar River sockeye salmon were tested for IHN virus by examining kidney, spleen, whole milt, seminal plasma, and homogenized sperm. In the 1983 brood year, we tested 15 males from this population, using spleen and whole milt, and in the 1984 brood year, we tested 15 males using kidney, spleen, and whole milt.

Male steelhead trout being used as brood stock in 1983 at the Round Butte Hatchery (Portland General Electric and Oregon Department of Fish and Wildlife) in Oregon were tested on two occasions. We tested the spleen and whole milt from 97 males on 1 February and the kidney, spleen, and whole milt from 50 males on 2 March. In 1985, male steelhead trout from this hatchery were again examined twice. We tested whole milt, kidney, and spleen from 50 fish on 29 January and whole milt and spleen from 132 fish on 6 February.

Sampling organs and fluids — Samples of milt, gills (including arch), spleen, kidney, liver, lower gut (3 cm above the anus), pyloric ceca, and brain were taken and processed as described by Mulcahy et al. (1984). For a comparison of procedures for processing milt, we tested whole milt samples from 12 sockeye salmon and then removed the sperm by centrifugation at 2000 × *g* for 10 min and decanted the seminal plasma and tested it by plaque assay. The pelleted sperm samples were then diluted 1:2 in cell culture medium, mechanically homogenized, and centrifuged at 2000 × *g* for 10 min; the supernatants were then tested by plaque assay.

Virus assay — We used the plaque assay (Burke and Mulcahy 1980) as modified by Mulcahy et al. (1982) with the EPC cell line (Fijan et al. 1983) to determine the levels of IHN virus in tissues and fluids. Briefly, the tissue samples were diluted 1:10 with Eagle's minimum essential medium (Auto-Pow, Flow Laboratories) without serum, buffered to pH 7.2 with tris(hydroxymethyl)aminomethane (MEMT), with the addition of 2.5 μg amphotericin B/mL (Fungizone, Grand Island Biological Company), 100 μg gentamicin sulfate/mL (United States Biochemical Corporation), 100 IU penicillin/mL, and 100 μg streptomycin/mL and mechanically homogenized. Homogenates were clarified by centrifugation at 2000 × *g* for 10 min. Replicate cell culture monolayers grown in eight-well multiplates (Lux No. 5218, Miles Scientific) were inoculated with 0.1 mL/well of undiluted fluid sample or tissue supernatant and further replicate monolayers with the same volume of serial $\log_{10}$ dilutions to 10^{-5}. Milt was assayed with dilutions to 10^{-3} without removal of sperm. After a 60-min adsorption period, assay plates were overlaid with MEMT containing 1% methylcellulose. Plaque plates were incubated for 7 d at 15°C before fixation and staining. Virus levels were calculated as plaque-forming units (pfu) per gram of tissue or per millilitre of fluid. Mean virus titers were calculated after individual titers were transformed to $\log_{10}$ values.

Results

Mean IHN virus levels in the visceral organs and fluids from four male sockeye salmon spawning in the Cedar River in 1980 were reported by Mulcahy et al. (1982). Only one fish had detectable IHN virus in whole milt despite the presence of high levels of virus in other organs (Table 1). The fish with virus in its milt was the only one having a viremia, with more than 5.00 $\log_{10}$ pfu/mL in the serum, and virus in the brain; high levels

TABLE 1. Levels of IHN virus in organs (log_{10} pfu/g) and fluids (log_{10} pfu/mL) of four male Cedar River sockeye salmon sampled on 13 November 1980.

Fish No.	Fluids		Organs						
	Milt	Serum	Gills	Spleen	Kidney	Liver	Lower gut	Pyloric ceca	Brain
1	0	0	6.49	5.76	3.70	3.54	4.84	6.41	0
2	3.48	5.30	6.80	7.08	5.89	7.30	6.99	7.48	3.00
3	0	0	4.99	0	0	2.00	0	4.23	0
4	0	0	8.04	7.20	4.69	7.30	7.34	7.60	0

TABLE 2. Incidences and mean titers (log_{10} pfu/g or log_{10} pfu/mL) of IHN virus in milt, kidney, and spleen from Cedar River sockeye salmon and Round Butte Hatchery steelhead trout. ND = not done.

Species	*n*	Milt		Kidney		Spleen		All (%)
		%	Titer	%	Titer	%	Titer	
Sockeye salmon								
1982	12	0	—	67	3.34	92	3.34	92
1983	15	7	2.85	ND	ND	60	4.99	60
1984	15	13	2.56	100	4.23	100	4.89	100
Steelhead trout								
1983 (1 February)	97	12	2.26	ND	ND	13	2.51	22
1983 (2 March)	50	6	2.99	44	4.18	58	3.54	60
1985 (29 January)	50	8	2.72	2	2.00	2	2.18	8
1985 (6 February)	132	4	3.08	ND	ND	5	4.41	8

TABLE 3. IHN virus incidences and titers (log_{10} pfu/g or log_{10} pfu/mL) in samples of kidney, spleen, and milt from spawning male Cedar River sockeye salmon during the 1982, 1983, and 1984 brood years.

1982[a]		1983		1984		
Kidney	Spleen	Milt	Spleen	Milt	Kidney	Spleen
0	3.90	0	0	0	2.70	6.26
0	2.60	0	0	0	3.00	5.70
3.00	2.95	0	5.53	2.61	7.87	7.52
4.49	4.79	0	0	0	4.91	6.38
3.51	4.04	0	4.45	0	1.70	2.00
1.70	2.81	0	4.49	0	4.53	4.51
2.93	1.70	0	0	0	6.04	7.63
3.04	4.83	0	2.00	0	3.98	4.92
0	0	0	4.67	2.51	7.11	7.32
3.40	4.34	0	0	0	3.30	4.38
0	0.70	0	0	0	3.30	2.40
4.72	4.18	0	1.70	0	5.91	5.67
—	—	2.85	9.36	0	1.70	4.30
—	—	0	5.96	0	3.60	2.18
—	—	0	6.72	0	3.78	2.18

[a]Virus was not isolated from whole milt, seminal plasma, or homogenized sperm.

TABLE 4. IHN virus titers (log_{10} pfu/g or log_{10} pfu/mL) in steelhead trout from the 1983 and 1985 brood years at Round Butte Hatchery in which virus was detected in samples of whole milt. ND = not done.

1983 brood year			1985 brood year		
Milt	Spleen	Kidney	Milt	Spleen	Kidney
	1 February			29 January	
1.87	0	ND	2.60	0	0
1.87	0	ND	2.11	2.00	0
1.70	0	ND	2.95	0	0
1.87	0	ND	1.23	0	2.18
3.36	0	ND		*6 February*	
1.40	0	ND			
3.45	0	ND	3.43	5.43	ND
2.11	0	ND	1.00	0	ND
1.40	1.70	ND	6.18	4.45	ND
2.23	2.60	ND	2.25	0	ND
1.87	2.18	ND	2.54	0	ND
3.98	4.11	ND			
	2 March				
3.57	4.32	2.48			
3.00	5.32	7.00			
2.40	8.08	7.90			

of IHN virus were also present in all other organs.

During the 3 yr of testing of male sockeye salmon from the Cedar River, IHN virus was isolated only rarely from milt samples, compared with the incidence in kidney or spleen, and the virus titer in milt was far lower than that in the organ samples (Table 2). The mean virus titers were higher in the spleen samples than in the kidney or milt samples (Table 2). Only 7 of the 42 fish examined in the 3 yr were negative in all samples. In 1982, no IHN virus was detected in whole milt samples, sperm-free seminal plasma, or mechanically homogenized sperm from 12 male sockeye salmon. The IHN virus was detected in whole milt samples from only 3 of the 42 sockeye salmon in this study (Table 3). In all three fish, virus titers in the spleen and kidney samples exceeded 7.00 log_{10} pfu/g, the highest virus titers from any of the fish (Table 2). In the one fish in 1983 with virus present in whole milt, the IHN

virus titer in the spleen was 9.36 $\log_{10}$ pfu/mL, an extremely high level.

The incidence of IHN virus in the male steelhead trout from Round Butte Hatchery was much lower than in the male Cedar River sockeye salmon (Table 2). During the first sampling in 1983, virus was detected in the whole milt but not in the spleen of 8 of 97 fish (Table 4). Virus was detected in both whole milt and spleen of four fish and in spleen but not whole milt from nine fish. In only two fish (both with negative whole milt) did virus titers in the spleen exceed 6.00 $\log_{10}$ pfu/g.

In the second sampling in 1983, consisting of 50 steelhead trout, IHN virus was detected in whole milt samples from only 3 fish (6%); the mean titer was 2.99 $\log_{10}$ pfu/mL (Table 4). In two of these fish, virus levels were higher than 7.00 $\log_{10}$ pfu/g in samples from either the kidney or spleen, or both. Different types of samples again yielded different infection rates and mean titers (Table 2). Virus was detected in the kidney but not in the spleen of one fish and in the spleen but not the kidney of eight fish.

Male steelhead trout being spawned at Round Butte Hatchery were again sampled twice in 1985. On 29 January, we examined samples of whole milt, spleen, and kidney of 50 fish, only 4 of which were infected with IHN virus (Table 2). Milt from all four fish plus samples from one spleen and one kidney (from different fish) were positive (Table 4). On 6 February, samples of whole milt and spleen from 132 males were tested and yielded 7 fish with IHN virus (Table 4). Milt samples from five fish and spleen samples from all seven were virus-positive (Table 4).

Discussion

The difference in IHN virus incidence between male and female salmonids of the same population may be an artifact of the use of milt for testing male fish. Spleen and kidney samples were clearly superior to milt for detection of IHN virus in male sockeye salmon and somewhat less so for steelhead trout, a finding that may reflect differences in virus replication between host species. Spleens were preferred to kidneys because spleens can be sampled more easily and the virus incidence and level were slightly greater in the spleen than in the kidney.

For critical IHN virus examinations of brood stocks, spleen, kidney, and milt samples from each fish should be used to increase the probability of detecting the virus. A disturbing aspect of this study was the finding of a number of steelhead trout in which IHN virus could be found in the milt but not in the spleen. If kidneys of these fish had been sampled in addition to the spleens, perhaps fewer of these infected fish would have been missed.

In most of the male sockeye salmon in this study in which IHN virus was detected in the milt, levels of virus in the corresponding kidney or spleen samples were very high (greater than 7.00 $\log_{10}$ pfu/g). Mulcahy and Pascho (1984) showed that IHN virus adsorbs to the surface of the head of salmonid sperm. The very high levels of virus in the visceral organs may indicate that the fish must produce massive numbers of virions in milt to saturate the virus binding sites on the sperm before the excess virus is available to be detected. When lesser levels of infection occur in fish, virus may be present in the milt samples, but is adsorbed tightly to the sperm and is therefore unavailable for infection of cell cultures. Low concentrations of IHN virus in whole milt might not be detected due to the toxicity of undiluted milt for fish cell cultures if the sperm are not first removed or the monolayers washed following adsorption. In 1982, IHN virus could not be isolated from milt samples taken from male sockeye salmon, some of which showed virus in spleen and kidney samples, even when the sperm cells were centrifuged from whole milt and homogenized and the homogenate and seminal plasma tested separately. Centrifuging milt samples to remove sperm and thereby reduce toxicity may actually remove the virus from the inoculum. Milt should not be used as the only type of sample from a population of any species of salmonid fish.

Differences in virus incidence and mean titers were seen between the brood years tested. Differences in virus incidence between sampling dates within the 1983 brood year were clearly seen in the steelhead trout population examined. No difference in virus incidence was seen between the two sample dates in 1985 — although mean titers were higher in the second sampling — but the second sampling was done earlier in 1985 than in 1983. The difference in infection rates within a brood year reinforces the need for sampling across the spectrum of the spawning run. It is especially important to include samples from the end of the spawning run because the incidence of virus infection is often higher than at the beginning of the run (Mulcahy et al. 1984).

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Increased Growth Rate in Atlantic Salmon Parr (*Salmo salar*) by Using a Two-Coloured Diet

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Fishes hunting by sight are known to pay a cost of confusion when faced with high densities of uniform food particles. Factors such as swarm size, density, and visual uniformity increase confusion. Therefore, it may be profitable in pisciculture to introduce food particles in low densities or to reduce the uniformity and density of each type of feed pellet. This was tested by feeding Atlantic salmon parr (*Salmo salar*) brown pellets, yellow pellets, or a mixed diet. Mean growth rates were significantly higher for those fish fed a mixed diet. Of the smaller fish in all groups, those in the mixed diet group showed the highest weight/length ratio. We suggest that small individuals have to pay more attention to conspecifics than do large ones, and thus tolerate less confusion when feeding. Larger individuals, tolerating higher confusion costs, achieve higher feeding rates in high densities of uniform feed pellets.

On sait que les poissons qui chassent à vue sont déroutés quand ils font face à des densités élevées de particules alimentaires uniformes. Des facteurs comme la taille, la densité et l'uniformité visuelle des proies viennent accroître la confusion. Il pourrait donc être rentable pour les pisciculteurs d'introduire les aliments en faible densité ou de réduire l'uniformité et la densité de chaque type de boulette de nourriture. Afin de vérifier cette hypothèse, on a nourri des tacons du saumon de l'Atlantique (*Salmo salar*) de boulettes brunes, de boulettes jaunes et d'un régime mélangé. Les taux moyens de croissance étaient nettement plus élevés chez les poissons nourris d'un régime mixte. Chez les petits poissons de chaque groupe, ceux appartenant au groupe nourri d'un régime mélangé montraient le plus haut rapport poids/longueur. Selon les auteurs, les petits individus doivent porter plus d'attention à leurs congénères que les gros et donc tolèrent moins de confusion au moment de l'alimentation. Les gros individus, qui tolèrent un niveau plus élevé de confusion, montrent des taux plus élevés d'alimentation à des densités élevées de boulettes de taille uniforme.

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In salmonid farming, large variability in individual growth is a problem of economic importance, at least partly because of an individual difference in feeding efficiency (Refstie and Kittelsen 1976).

Animals concentrate on profitable prey if its abundance reaches a certain threshold (Emlen 1966; MacArthur and Pianka 1966). However, as there are remarkable individual differences when feeding, individuals with low competitive abilities are not always able to select the optimal diet predicted for conditions of no competition (Rubenstein 1981; Milinski 1982).

Feeding in high densities of prey also reduces feeding efficiency and is termed the confusion effect (Miller 1922; Milinski 1977). The fish hesitates before attacking and has difficulties in aiming at one target which is quickly masked by other similar targets (Milinski 1977). The existence of such an effect is supported by field observations with swarming prey (Allen 1920; Mosebach-Pukowski 1937; Eibl-Eibesfeldt 1962; Hobson 1968; Potts 1970; Radakov 1973).

The following characteristics of a swarm enhance the confusion effect: (1) number of individuals in the swarm (Welty 1934; Neill and Cullen 1974); (2) number of swarm members per volume of swarm (Milinski and Curio 1975; Milinski 1977; Morgan and Ritz 1985); and (3) uniformity of members within the swarm (Muller 1978; Ohguchi 1978).

However, Milinski (1979) has suggested that feeding in dense areas of prey may become possible if other costs, such as risk of predation (Milinski and Heller 1978), which conflict with feeding activity, are low. Less documented is the influence of intraspecific aggression on the cost of confusion and how this can influence competitive success, expressed as the individual's growth rate. Salmon parr living in densities typical for commercial fish farming are known to behave agonistically (Blaxter 1975). The ratio between performed and received aggressive acts is highest for large Atlantic salmon parr (*Salmo salar*) at high densities, and compared with large parr the growth of small parr in a population becomes slower with increasing density (Ferno and Holm 1986).

Our objective was therefore to test the hypothesis that aggression/competition disproportionally reduces the ability

of different-sized fish to feed on confusing densities of prey. In the present experiment, Atlantic salmon parr of various sizes were held in tanks and fed artificial food in fairly high densities, as in traditional aquaculture. The confusion was presumed reduced in one group of tanks by presenting a mixture of brown and yellow pellets.

Methods

The juvenile Atlantic salmon used in the experiments stemmed from six mothers and two fathers. Sibling groups, with known length and weight distributions, were divided equally into nine experimental tanks at the start of the experiment.

Number varied between 1436 and 1339 fish in each tank and was never more than 803/m^3 or 7.02 kg fish/m^3. Fish fork length varied between 48 and 98 mm at the start of the experiment. All fish were in their second year, but none were smoltifying. The experimental arenas were nine dark-green, circular, covered tanks each measuring 1.5 m in diameter. Water depth was 80 cm. River water neutralized with a NaOH solution to pH 6.3 flowed continuously into the tanks and the water was changed on average every 3 h.

The experiment was started 18 January 1985 and terminated 82 d later. Temperature varied between 2 and 3°C in the first 30 d and increased gradually to 7°C by the end of the experiment.

The fish were exposed to continuous light from a 60-W bulb placed 30 cm above the surface during the experimental period. They were fed with an Ewos automatic feeder. Since the water flow was directed from the feeder towards the light bulb, the food particles were best illuminated just after they were introduced into the tanks.

The experiments consisted of three groups of three tanks each, run in parallel. In one group, the fish were fed a mixed diet consisting of 30% yellow pelleted food and 70% brown, the natural colour. In the other groups the fish were fed either homogeneous brown or yellow pellets. All fish were fed on a diet of brown pellets until the experiment started. The fish were fed to excess, and there were no significant differences in the amount of food used between the experimental groups. Mortality was low, ranging from 0 to 14 individuals in each tank.

Small amounts of diethyl ether were added to all food pellets to get a thin oil layer at the surface of the food particles, thereby making colour coating easier. Two percent (weight) curcumin E100 was used to give pellets a light yellow colour with a greenish tint. The diethyl ether was dried off by storing pellets at 25°C for at least 24 h before it was introduced to the tanks. Since both brown and yellow pellets were treated with diethyl ether, and curcumin has no additional growth effect (Bhuvaneswaran et al. 1963), food value was equal for all diets.

The size of the granulated food particles (Ewos No. 3 salmon feed) averaged 2.4 mm. Particle size distribution was equal throughout the experiment. At least 96% of the particles were within the acceptable size range of 0.018–0.051 times the fork length of the salmon, and all particles were of the size that elicits a response (Wankowski 1979).

At least 400 particles were offered to the salmon every 10 min. The particles were released over a 3-s interval for each feeding period. Throughout the experiment, more food particles were added to the tanks than the fish needed. Consequently, many particles were not eaten before reaching the bottom of the tank, where they were left uneaten by the fish. Presumably they could have been eaten from the bottom, but unlike, for instance trout, salmon parr normally do not pick up food from the bottom (J.C. Holm and P. J. Jakobsen, unpubl. data).

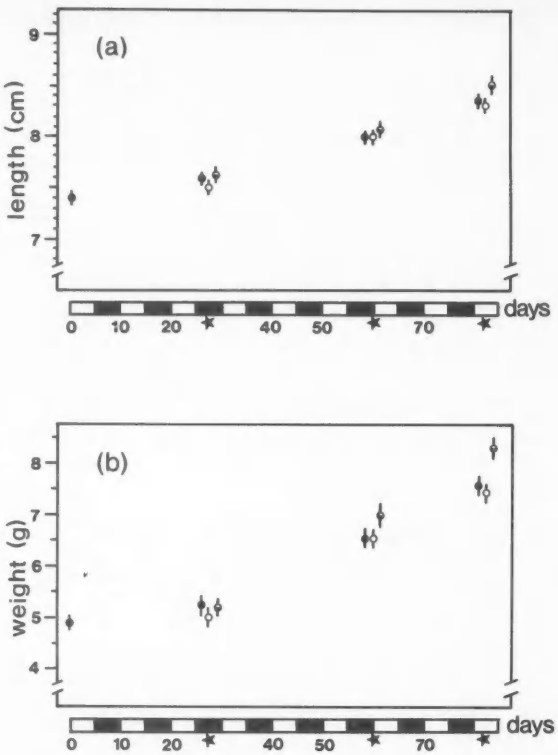

FIG. 1. (a) Mean lengths and (b) mean weights of fish fed yellow (open circles), brown (solid circles), and mixed (half-solid circles) coloured food particles. The 95% confidence intervals are indicated.

The water level in the tanks was lowered when removing samples of fish from the tanks for measurements to diminish sampling biases resulting from any size-dependent differences in avoidance. Sampled fish were anaesthetized with benzocaine solution. Fork length and weight were measured for at least 100 individuals from each tank each time, except for the final measurement when about 250 were sampled from each tank. Measurements were taken four times at approximately 1-mo intervals.

Fork lengths (centimetres) and weights (grams) of the fish in each tank were log–log regressed for each sampling according to

$$\text{Weight} = a \times \text{length}^b$$

where a is the intercept and b is the slope; b is a measure for the weight/length ratio between the fish from each tank.

Results

In the three tanks where salmon were offered a mixed diet, the increases in both length and weight in the first 82 d were

TABLE 1. Weight/length regressions for the three different treatments.

	Yellow				Brown				Mixed			
	a	*b*	*r*	*n*	*a*	*b*	*r*	*n*	*a*	*b*	*r*	*n*
Day 1					0.018	2.78	0.95	808				
Day 27	0.013	2.92	0.96	300	0.014	2.89	0.95	300	0.018	2.76	0.94	300
Day 60	0.016	2.86	0.97	310	0.015	2.89	0.96	310	0.015	2.88	0.97	296
Day 82	0.012	2.98	0.96	745	0.013	2.94	0.96	749	0.020	2.78	0.97	760

higher than for those fed a homogeneously coloured diet of brown or yellow pellets (Fig. 1). Differences in weight were significant 60 d after the start ($P > 0.05$, Mann–Whitney *U*-test). Those fed either brown or yellow food did not differ in size at any time ($P > 0.05$). The slow growth in the first part of the experiment was probably due to the low temperatures.

At the end of the experiment, the fish exposed to a mixed diet had the lowest value of regression coefficient *b* and the highest values of the intercept *a* ($P < 0.024$, Mann–Whitney *U*-test). Relative to larger fish, small fish in these tanks therefore had a higher weight than similar fish offered homogeneously coloured food (Table 1). There were no significant differences between the fish fed either homogeneously coloured yellow or brown food particles.

Discussion

Atlantic salmon parr showed a higher increase in both length and weight when fed a mixed colour diet than when fed uniformly coloured pellets. Small fish, in particular, tended to grow better on the mixed diet than those fed homogenously coloured pellets, thus indicating a difference in ability of small and large fish to feed on confusing prey densities.

Differences in growth cannot be due to differences in food quality, as neither caloric value nor essential trace elements were added by the colouring agent, although the taste may have been affected. Growth rates were not significantly different in the two groups fed yellow or brown food pellets alone. For this reason, neither of the food types seems to be more profitable when homogeneously introduced to the fish.

Yellow food particles may be more conspicuous against a background of brown particles. Compared with those fed a homogeneously coloured diet, this phenomenon should increase growth rate of all fish. However, in this experiment, small fish fed a mixed diet showed a higher weight/length relation relative to the large ones fed the same diet.

A general increase in feeding motivation caused by mixing of differently coloured food particles (Rolls et al. 1982) can possibly also increase growth of all salmon. However, this can not explain the lower slope of the weight/length regression in those fish fed mixed food, showing higher growth of the smallest fish relative to the small fish fed homogenously coloured food. This is because all sizes of fish should increase feeding motivation.

The slightly better growth of large salmon fed a mixed diet also indicates possible reduced costs or more intake when feeding on a mixed diet. Since mixing of food types lowers the density of each equal looking food type, an obvious explanation is that of Milinski and Heller (1978) and Morgan and Ritz (1985) who found that animals have to pay a confusion cost when feeding in high densities of prey, and when paying attention to other stimuli, they are effectively feeding in low prey densities (Milinski 1979). Ferno and Holm (1986) found that the ratio between the number of performed and received aggressive actions became higher for large parr at high densities of fish. Further, they found that small fish grew slower at these high densities and suffered generally from a higher mortality. Hence, small fish, in particular, have to pay attention to others, thereby increasing the confusion and reducing the opportunity of feeding in areas of high food densities. Under such conditions, a mixed diet allows a higher feeding rate, since the density of uniform food particles is lowered, thus reducing the confusion cost.

Dominance in Atlantic salmon parr is related to size at densities similar to our experiment (Ferno and Holm 1986), implying that larger fish are more capable of feeding in high food densities. When uniform particle density is decreased, this could explain the better growth rate of the smallest individuals in the mixed diet group relative to small fish fed homogeneously.

This obviously has implications in pisciculture. Feeding regimes favouring an improved and more stable growth rate promote a better and more consistent quality of fish. The decreased need for size grading the fish also reduces labour cost. Additionally, mixing of food particles gives the fish an opportunity to consume a higher proportion of the offered food and may help the fish farmer to optimize production while reducing pollution from waste food.

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Winter and Spring pH Depressions in Northern Wisconsin Lakes Caused by Increases in pCO_2[1]

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Seasonal variation in pH in six clearwater northern Wisconsin lakes (mean pH 5.9–7.8; mean total alkalinity 9–830 $\mu eq \cdot L^{-1}$) encompasses an annual range of 1.0–1.5 units in each lake, with lowest values characteristically occurring during the late winter and early spring. In detailed investigations of one lake, we evaluated strong acid inputs, shifts in pCO_2, and changes in organic acids as possible mechanisms for pH depression. Our results indicate that seasonal pH depressions are caused largely by pCO_2 increases under the ice. Despite an acidic snowpack the pH depression could not be attributed to input of acid meltwater because total alkalinity did not change in the lake. Our results emphasize the importance of using measurements other than pH in investigating the causes of acid dynamics of natural waters.

La variation saisonnière du pH de chacun de six lacs à eau transparente du nord du Wisconsin (pH moyen de 5,9 à 7,8; alcalinité totale moyenne de 9–830 $\mu eq \cdot L^{-1}$) se situe dans une gamme annuelle de 1,0 à 1,5 unités. Les valeurs les plus faibles sont, de façon caractéristique, notées à la fin de l'hiver et au début du printemps. Au cours

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d'une étude détaillée de l'un des lacs, les auteurs ont trouvé que des apports acides importants et des variations du pCO_2 et des teneurs en acides organiques pouvaient être les mécanismes expliquant la baisse du pH. Les résultats obtenus montrent que les baisses saisonnières du pH s'expliquent en grande partie par des augmentations du pCO_2 se produisant sous la glace. En dépit de la présence d'une masse de neige acide, la baisse du pH n'a pu être attribuée à l'apport d'eaux de fonte acides car l'alcalinité totale ne variait pas au sein du lac. Les résultats obtenus soulignent l'importance d'utiliser d'autres mesures que le pH pour l'étude des causes de la dynamique de l'acidité dans les eaux naturelles.

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The pH of natural waters can be highly dynamic on daily (Schindler et al. 1972; Schindler 1974), seasonal (Hutchinson 1967), and long-term (National Academy of Sciences 1986) time scales. Such shifts in hydrogen ion concentration may exert substantial influence over chemical and biological properties of aquatic ecosystems (Sillen 1967; Stumm and Morgan 1981; Magnuson et al. 1984a; Schindler et al. 1985). In several instances, seasonal and long-term increases in hydrogen ion concentration have been attributed to an influx of strong acids that are anthropogenic in origin (National Academy of Sciences 1986). In particular, a characteristic pattern of spring pH depression due to meltwater inputs of anthropogenic acids has been described for several systems (Henrikson and Wright 1977; Jeffries et al. 1979; Siegel 1981; Cadle et al. 1984). Here we report 1.0–1.5 unit pH depressions during winter and spring in several northern Wisconsin lakes that are attributable to natural increases in pCO_2 rather than influxes of mineral acids.

Winter and spring pH depressions can be caused by three likely mechanisms: (1) changes in alk_{tot} caused by strong acid input from meltwater produced by an acid snowpack, (2) increase in pCO_2 under ice, and (3) accumulation of weakly ionizable organic acids. Any of these factors may predominate in some aquatic systems. Input of strong acid from the atmosphere, meltwater, or watershed can decrease alk_{tot} and pH (Jeffries et al. 1979; Henrikson and Wright 1977; Stumm and Morgan 1981; Kelso et al. 1986). However, reduction reactions in anoxic porewaters or hypolimnia can increase alk_{tot} and pH (Cook et al. 1986; Kelly et al. 1982; Kuivila and Murray 1984). Changes in pCO_2 brought about by production and respiration can alter pH (Schindler et al. 1972; Schindler 1974). Finally, influxes of organic acids can reduce pH in peatland-dominated systems (Gorham et al. 1985).

To test for pH depressions caused by strong acid inputs, we examined seasonal patterns of alk_{tot}, since changes in pCO_2 and dissolved organic carbon (DOC) do not directly change concentrations of nonprotolytic cations and anions and, therefore, would not affect alk_{tot}. To evaluate the importance of changes in pCO_2, we calculated pCO_2 dynamics two ways: (1) from pH and alk_{tot} and (2) from direct analyses of changes in dissolved oxygen assuming that O_2 depletion is a predictor of CO_2 accumulation. We examined seasonal trends in DOC to evaluate the effects of organic acids. Through this combination of analyses we determined the relative importance of each of these mechanisms influencing pH depressions in northern Wisconsin lakes.

Methods

We studied the mechanisms controlling pH dynamics in Little Rock Lake, the site of an ongoing controlled acidification experiment (Brezonik et al. 1986). Intensive chemical measurements have been made since October 1983. To test the generality of the seasonal pH trends observed in Little Rock Lake, we have included a longer term pH record from five other lakes studied as part of the Northern Lakes Long Term Ecological Research (LTER) Project (Magnuson et al. 1984b). Measurements on the LTER lakes began in July 1981, but measurement frequency for certain chemical parameters (alk_{tot}, major ions, DOC) is less than that for Little Rock Lake. The data collected at the six study lakes were not originally intended for the analyses presented here, and therefore have some limitations, but we believe that they are sufficient to support our conclusions.

Our study lakes are located in the Northern Highland Lake District in northern Wisconsin (46°00′N, 89°37′W). In this region, preCambrian igneous/metamorphic bedrock is overlain by about 40 m of noncalcareous, sandy tills and outwash (Kenoyer 1986; Okwueze 1983). The study sites are representative of clearwater lakes in the district and range in mean pH from 5.9 to 7.8, in mean alk_{tot} from 9 to 830 $\mu eq \cdot L^{-1}$, and in mean specific conductance from 11 to 85 $\mu S \cdot cm^{-1}$ and include both seepage and drainage lakes (Table 1).

In Little Rock Lake, temperature, dissolved oxygen, pH, and alk_{tot} were measured every 2 or 3 wk in the north basin during the ice-free season and monthly during periods of ice cover. Additional weekly pH measurements were made during March and April 1985. Major ions were measured monthly. We measured DOC five times between May 1984 and April 1985. In the five LTER lakes, pH was measured every 2–4 wk.

All water samples were taken during the day from three to seven depths using a peristaltic pump and Tygon tubing. We sampled above the deepest part of each lake. Samples for pH and alk_{tot} were pumped unfiltered into 20-mL polyethylene vials with displacement caps which prevented gas exchange. Samples for major ions were pumped through an in-line 0.4-μm Nuclepore filter. Samples for DOC were collected unfiltered in amber glass bottles and passed through 0.45-μm Millipore filters in the laboratory. All samples were kept cold and dark from collection until analysis.

We analyzed pH in the laboratory within 5 h of collection using a Radiometer-Copenhagen PHM 84 meter and Corning semi-micro combination electrodes. Samples were measured without stirring, at room temperature, and in an apparatus designed to minimize CO_2 exchange with the atmosphere. Water temperature during the winter and early spring was near 3°C, and we assumed that the temperature influence on pH was small compared with the observed seasonal changes.

TABLE 1. Limnological characteristics of the study lakes.

Lake	Lake surface area (ha)	Lake type[a]	Mean depth (m)	Mean pH	Mean total alkalinity ($\mu eq \cdot L^{-1}$)	Mean specific conductance ($\mu S \cdot cm^{-1}$)	Secchi disk depth (m)
Little Rock	9.8	S	3.8	5.90	28	11	4.6
Allequash	168	D	2.9	7.59	763	82	3.0
Big Muskellunge	396	S	7.5	7.40	371	43	7.2
Crystal	36.7	S	10.4	6.03	9	14	8.3
Sparkling	81.4	S	10.9	7.63	568	72	6.6
Trout	1608	D	14.6	7.79	830	85	4.6

[a]S = Seepage lake (no surface inlet or outlet); D = drainage lake (at least one permanent inlet and/or outlet).

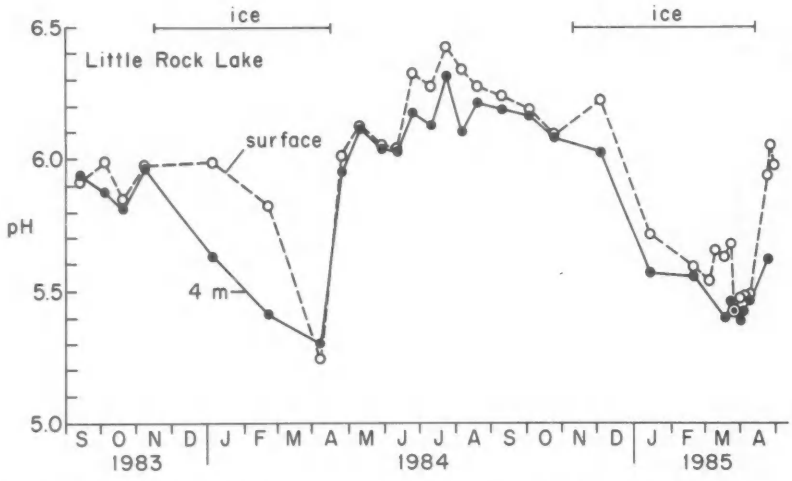

FIG. 1. Surface and 4-m pH in Little Rock Lake between September 1983 and April 1985.

Alk_{tot} was analyzed within 24 h on samples at room temperature using Gran titration between pH 4.5 and 3.5. Agreement between measured values of alk_{tot} and values calculated as the difference between base cations and anions was excellent (89% fell within 10 $\mu eq \cdot L^{-1}$ and 96% within 15 $\mu eq \cdot L^{-1}$; $n = 117$). Therefore, in the few cases in which alk_{tot} was not measured, alk_{tot} was calculated from the difference between base cations and anions.

Base cations (Ca^{2+}, Mg^{2+}, K^+, and Na^+) were analyzed using flame atomic absorption (American Public Health Association et al. 1980). SO_4^{2-} was analyzed by the methylthymol blue method and Cl^- by the ferricyanide method, both on an auto analyzer (American Public Health Association et al. 1980). DOC was measured on a Barnstead total carbon analyzer. We determined temperature and dissolved oxygen using a Montedoro–Whitney CTU-3B temperature meter and a YSI model 57 or 58 oxygen meter.

We calculated pCO_2 from pH, carbonate alkalinity, and temperature using equations given in Stumm and Morgan (1981) and dissociation constants given in Truesdell and Jones (1974). Little Rock Lake contains an average of 9.2 ± 8.6 $\mu eq \cdot L^{-1}$ (mean and standard deviation of four measurements) of noncarbonate alkalinity, most likely due to weak organic acids (Cook et al. 1987). Therefore, we subtracted 9 $\mu eq \cdot L^{-1}$ from total alkalinity to estimate carbonate alkalinity. Although uncertainty in our estimate of carbonate alkalinity introduces an error in our calculation of pCO_2, the error is much less than the range of pCO_2 values calculated for Little Rock Lake and does not affect our conclusions. We also recognize that electrode measurement of pH may introduce systematic errors due to interactions with DOC (Herczeg and Hesslein 1984; Herczeg et al. 1985). Any systematic error may create large biases in calculations of pCO_2. However, we are interested in changes in pCO_2, not absolute values per se, so our conclusions concerning the causes of the pH depressions will not be affected by pH measurement biases.

We also computed pCO_2 increase in Little Rock Lake using whole-lake winter O_2 depletion data and assuming both an equimolar ratio of CO_2 release and O_2 depletion and the often used ratio of 0.85 (Ohle 1952; Hutchinson 1957). This ratio varies widely among lakes (Rich 1975; Rich and DeVol 1978) and is often greater than 0.85. Measured values in Dunham Pond, Connecticut, were approximately 1.0 in the early part of winter (Rich 1979). O_2 depletion was estimated from measurements made on 3 December 1984 and 2 April 1985. Masses of O_2 and hydrogen ion in the lake were calculated as the product

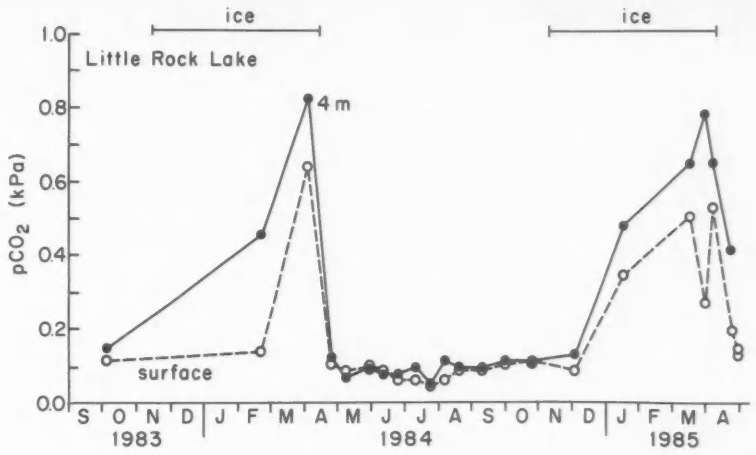

FIG. 2. Calculated values of pCO_2 at ambient temperature at the surface and at 4 m in Little Rock Lake.

TABLE 2. Comparison of whole-lake hydrogen ion concentration change observed and that calculated from whole-lake O_2 depletion in Little Rock Lake.

Parameter	3 December 84	2 April 85	Change
Measurements			
O_2 (mmol·L^{-1})	0.38	0.16	0.22
pH	6.12	5.43	0.69
H^+ (μmol·L^{-1})	0.76	3.72	2.96
Total alkalinity (μeq·L^{-1})	30	27	3
Calculations			
Carbonate alkalinity (μeq·L^{-1})[a]	21	18	3
CO_2 gain (mmol·L^{-1})			0.22[b] 0.19[c]
H^+ change (μmol·L^{-1})			2.96[b] 2.59[c]
Calculated H^+ change/measured H^+ change			
H^+ change			1.00[b] 0.87[c]

[a]Calculated assuming noncarbonate alkalinity = 9 μeq·L^{-1} (see text).
[b]Calculated assuming CO_2 release/O_2 uptake = 1.0.
[c]Calculated assuming CO_2 release/O_2 uptake = 0.85.

of concentration and volume at each depth sampled (Wetzel 1983). The whole-lake, volume-weighted average concentration was calculated from the mass in the lake and the volume of the lake.

Results

The pH of Little Rock Lake changed markedly with season (Fig. 1). Values at the surface and at 4 m averaged slightly above 6.0 during open-water periods, but declined soon after ice covered the lake. The lowest observed pH level, about 5.3, occurred just before the lake opened in the spring. Within days of ice-out the pH returned to near 6.0. In both winters the pH declined more rapidly at 4 m than at the surface.

Calculated values of pCO_2 in Little Rock Lake increased during the period of pH depression (Fig. 2). The values of pCO_2 increased sooner and peaked higher at 4 m than at the surface. Increases in pCO_2 resulting from respiration, calculated assuming ratios of CO_2 production and O_2 depletion of 0.85 and 1.0, can account for 87 and 100%, respectively, of the measured hydrogen ion change in Little Rock Lake in the winter of 1984–85 (Table 2).

In contrast with pCO_2, alk_{tot} showed little change or possibly a slight increase during the winter months (Fig. 3). Although alk_{tot} did decrease on 3 April 1985, simultaneous decreases in the sum of base cations and SO_4^{2-} suggest dilution by meltwater rather than strong acid input. Likewise, DOC data, although limited, suggest no increase in organic acidity under ice cover (Fig. 3). A lack of important DOC influence on overall pH change is also indicated by calculations suggesting that even a doubling of DOC concentration would decrease pH only 0.3 unit in Little Rock Lake (R. B. Cook, unpubl. data).

The five LTER lakes showed similar pH patterns to those in Little Rock Lake. However, the lakes vary in their annual range of pH and in the extent of pH depression that occurs under ice cover (Fig. 4). In Allequash Lake, pH is typically 1–2 units higher than Little Rock Lake; its mean depth is similar to Little Rock Lake; but its general chemistry differs greatly (Table 1). In contrast, Crystal Lake, which is similar chemically to Little Rock Lake, but much deeper, exhibits relatively little decrease in pH under ice cover.

Discussion

Four lines of evidence support our conclusion that changes in pCO_2, rather than increases in strong mineral or weak organic acids, account for the depression of pH in Little Rock Lake. First, pH started to decrease soon after the ice formed a barrier to gas exchange with the atmosphere, allowing for the

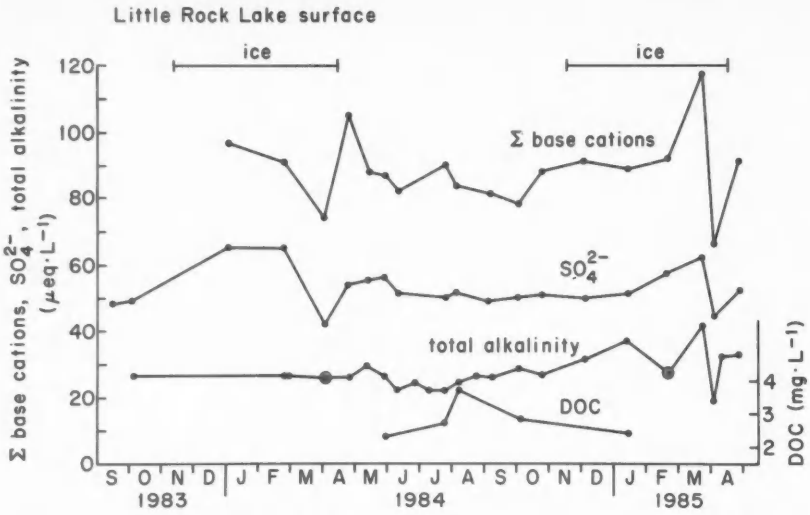

FIG. 3. Measured values of sum of base cations, SO_4^{2-}, total alkalinity, and dissolved organic carbon (DOC) at the surface of Little Rock Lake. Circled values for total alkalinity were calculated from the difference of base cations and anions (see text).

buildup of pCO_2. Second, the pH declined first in deeper water where sediment respiration has a greater influence on water column chemistry because of the small water volume to sediment area ratios (Hutchinson 1941; Hesslein 1980). Furthermore, the amount of O_2 depletion accounted for all of the observed pH depression. Third, alk_{tot} did not decrease and DOC did not increase during periods of low pH, precluding the importance of strong mineral or weak organic acids. Finally, the pH returned to near 6.0 within days after ice breakup. Presumably, degassing of CO_2 from the lake occurred much faster without ice cover.

The snowpack in northern Wisconsin is known to be acidic. The 1979–82 average pH of snowfall at Trout Lake is 4.57 (Glass and Loucks 1986). However, except for the snow that falls directly on the lake, it appears that very little of the acid snowmelt reaches the lake. Early, heavy snowfalls in the region insulate the sandy soil, so that the soil typically does not freeze or freezes only to a shallow depth. Meltwater quickly infiltrates the soil (T. K. Kratz, pers. obs.) and the acidity is quickly neutralized by reactions occurring in the soil or groundwater (Kenoyer 1986). For strong acids from snowmelt to cause the pH decline observed in Little Rock Lake, a decline in carbonate alkalinity of about 20 $\mu eq \cdot L^{-1}$, or the equivalent of 3 m of pH 4.57 meltwater, would be required. This amount of water is at least an order of magnitude greater than the amount of precipitation occurring during the ice-covered season.

pCO_2 dynamics are also the likely cause of seasonal pH patterns observed in the LTER lakes. Although alk_{tot} of the LTER lakes was not measured at a sufficient frequency to assess changes in pCO_2 directly, it seems likely that strong acid inputs are not important. The magnitude of pH depression in the winter is too large to be caused solely by strong acid inputs. For example, for strong acids to cause a decline in pH from 8.2 to 6.8 in Allequash Lake ($alk_{tot} \approx 800\ \mu eq \cdot L^{-1}$), a reduction in alkalinity of 760 $\mu eq \cdot L^{-1}$, or the equivalent of 30 m of pH 4.0 meltwater, would be required. The same depression requires an increase of pCO_2 to about 19 times atmospheric levels, similar to the increase observed in Little Rock Lake. Likewise, since the LTER lakes occur in the same climatic and geological setting as Little Rock Lake and since Little Rock Lake's chemistry indicates a potentially high susceptibility to strong acid inputs, the lack of a strong-acid influence on pH depression can justifiably be extrapolated to the LTER lakes, and perhaps most lakes in the region.

The similarity of the pattern of pH depression in Allequash and Little Rock lakes suggests that lake morphometry may be as or more important than general water chemistry in determining the extent of CO_2-induced pH depression that occurs in a particular lake. Shallow lakes with organic-rich sediments would be more likely to experience increases in near surface pCO_2 under the ice, and hence exhibit late winter pH depressions, than would deeper lakes with less organic sediments.

The biological consequences of pCO_2-induced pH depressions are unclear. The values we observed in Little Rock Lake, as low as 5.3, are similar to those which induced biotic effects in experimentally acidified Lake 223 (Schindler et al. 1985). These low-pH (or high-CO_2) periods, in conjunction with other factors (Tonn and Magnuson 1982; Rahel 1984), may influence community assemblages of fishes and other aquatic organisms in northern Wisconsin lakes.

Our results underscore the dynamic nature of acid conditions in lakes and suggest that estimates of pH based on one or a few data points are valid, at best, only for the season in which they are made. Furthermore, pH values determined during periods when rapid pH changes are likely, e.g. October through June in some northern Wisconsin lakes, should be interpreted with caution.

Given the controversy over lake acidification caused by fossil fuel emissions, natural pH fluctuations must be distinguished from those caused by anthropogenic factors. Measurements of pH alone, although important, must be combined with more detailed chemical analyses to assess the mechanisms that control acid conditions.

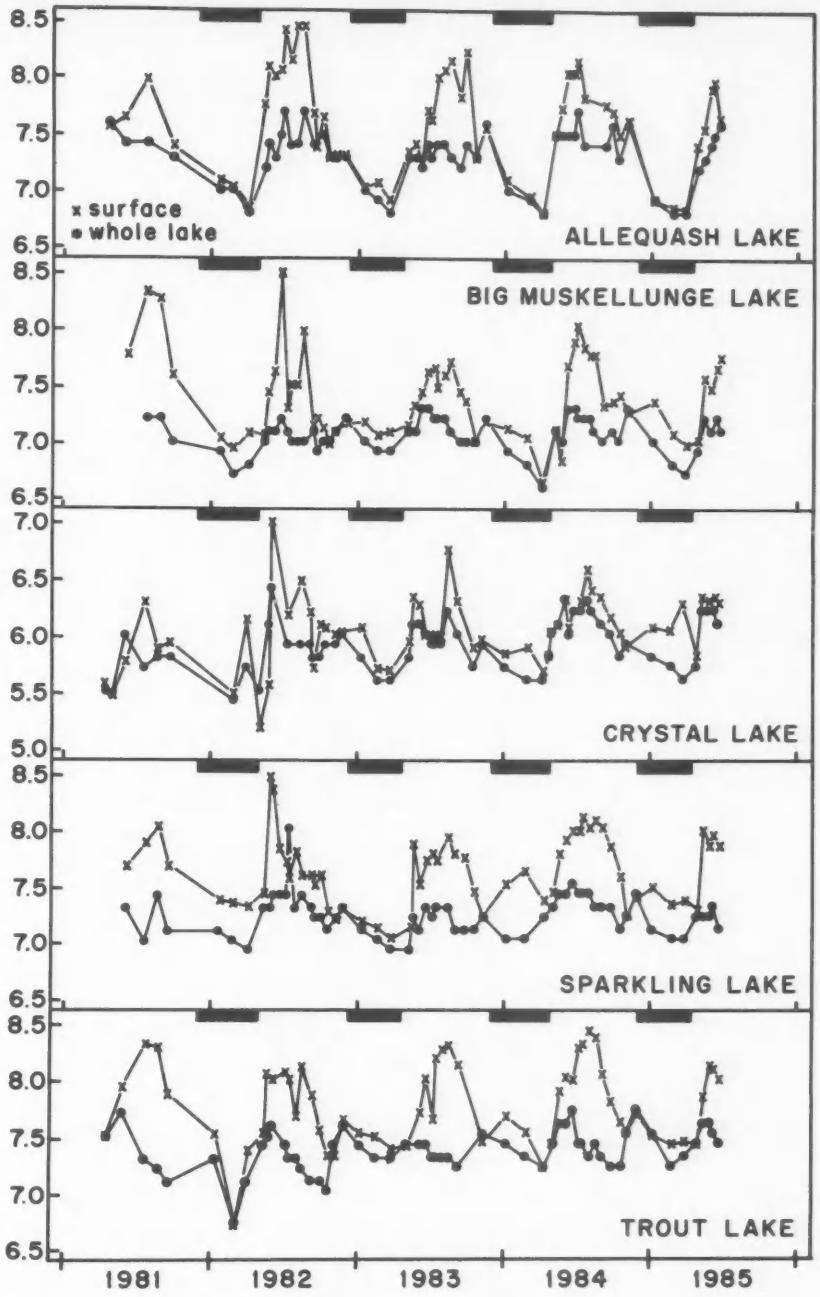

FIG. 4. Surface and whole-lake pH in five LTER study lakes from 1981 to June 1985. Solid bars indicate ice-covered periods.

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Preexposure and Subsequent Resistance to Lead in Yearling Brook Trout, *Salvelinus fontinalis*

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Tang, Y., and E. T. Garside. 1987. Preexposure and subsequent resistance to lead in yearling brook trout, *Salvelinus fontinalis*. Can. J. Fish. Aquat. Sci. 44: 1089–1091.

Potential for acclimation of brook trout, *Salvelinus fontinalis*, at sublethal levels of dissolved lead was measured. Samples of yearlings (19.2 ± 6.1 g) were preexposed continuously to environmentally realistic sublethal levels (10, 24, and 37 μg Pb/L) for 10, 20, 30, and 40 d and subsequently exposed to a lethal level (2 mg Pb/L), during which the incidence of mortality was recorded. Survival intervals of fish preexposed to 10 μg Pb/L were not significantly different from those preexposed to tap water (<2 μg Pb/L) in each preexposure interval. Fish preexposed to 24 μg Pb/L for 10 and 20 d were less resistant but returned to normal resistance after 30 and 40 d of preexposure. Fish preexposed to 37 μg Pb/L had significantly shorter survival intervals than those preexposed to tap water in each preexposure interval. The maximum acceptable toxicant concentration (MATC) of lead for brook trout is set between 24 and 37 μg Pb/L.

Les auteurs ont quantifié le potentiel d'acclimatation de l'omble de fontaine (*Salvelinus fontinalis*) à des teneurs sublétales en plomb dissous. Des échantillons de tacon d'un an (19,2 ± 6,1 g) ont été continuellement exposés à des teneurs sublétales présentes dans l'environnement (10, 24 et 37 $\mu g \cdot L^{-1}$ de Pb) pendant 10, 20, 30 et 40 j puis exposés à des niveaux létaux (2 $mg \cdot L^{-1}$ de Pb), période au cours de laquelle l'incidence de mortalité a été enregistrée. Chez les poissons préexposés à 10 $\mu g \cdot L^{-1}$ de Pb, la survie n'était pas nettement différente des poissons préexposés à de l'eau de robinet (<2 $\mu g \cdot L^{-1}$ de Pb) pendant chaque intervalle de préexposition. Les poissons préexposés à 24 $\mu g \cdot L^{-1}$ de Pb) pendant 10 et 20 j étaient moins résistants; leur résistance est redevenue normale après 30 et 40 j de préexposition. Les poissons préexposés à 37 $\mu g \cdot L^{-1}$ de Pb montraient des intervalles de survie nettement plus courts que ceux préexposés à de l'eau de robinet pendant chaque intervalle de préexposition. La concentration maximum acceptable de produits toxiques (MATC) du plomb pour l'omble de fontaine varie donc de 24 à 37 $\mu g \cdot L^{-1}$ de Pb.

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Gradual increases in concentration of potentially toxic heavy metals in freshwater ecosystems allow certain organisms to become acclimated to those and other metals. Increased tolerance and resistance resulting from exposure to elevated metal concentrations was first reported by King (1937). Subsequently, similar phenomena were reported, including acclimation to zinc (Spehar 1976), cadmium (Pascoe and Beattie 1979; Duncan and Klaverkamp 1983), mercury (Bouquegneau 1973), copper (McCarter and Roch 1983), and aluminum (Orr et al. 1986). However, in some instances, preexposure of fish to sublethal levels of pollutants would sensitize rather than acclimate them to the pollutants. Dixon and Sprague (1981) found that copper acclimation caused increased sensitivity to zinc and, at some acclimation concentrations, also increased sensitivity to copper. Unfortunately, some of these studies were side-issues in larger studies and did not report whether mortality occurred during the period of preexposure; thus, the results are doubtful because the tests may have been conducted on resistant individuals which survived the preexposure, resulting in selection of more tolerant fish. Most of the work used sublethal levels of toxicants as the preexposure or acclimation concentrations, but the concentrations are still higher than those that commonly occur in natural waters.

It was reported that natural lead concentrations in samples from about 2500 locations in Canada, from rivers, lakes, wells, and other groundwater, are usually less than 10 μg/L with a few ranging to 30 μg/L (Leah 1976). Because of the continuing anthropogenic release, concentrations of lead are steadily increasing in rivers, lakes, and oceans (Holcombe et al. 1976). Therefore, it is necessary to know if aquatic life could become acclimated to this toxic metal. Acclimation to lead has been demonstrated for some invertebrates (Brown 1976; Brown and Chow 1977; Fraser et al. 1975) and some vertebrates (Hapke 1977), but not for fishes.

The objectives of this study are to determine whether or not preexposure of fish to environmentally realistic sublethal levels of lead increase the survival interval of fish upon subsequent acute lead exposure and the extent to which survival intervals of fish change as a result of various preexposure levels and preexposure periods.

Materials and Methods

The experimental procedure involved preexposure of brook trout, *Salvelinus fontinalis*, to sublethal levels of lead (10, 24,

TABLE 1. Common logarithms of the survival interval (hours) of brook trout killed by lead (2 mg/L) after preexposure to 10, 24, and 37 μg Pb/L and tap water (<2 μg Pb/L) for 10, 20, 30, and 40 d. Values are means ± SD; $N = 60$. Two-level nested ANOVA followed by a Student–Newman–Keul test for comparisons of means were used to analyze the differences of survival intervals among the treatments. Means that are underlined are not significantly different ($P > 5\%$).

Days of preexposure	Control	10 μg/L	24 μg/L	37 μg/L
10	2.198 ± 0.095	2.190 ± 0.103	2.072 ± 0.122	2.013 ± 0.140
20	2.174 ± 0.123	2.125 ± 0.117	2.057 ± 0.170	1.895 ± 0.187
30	2.170 ± 0.131	2.184 ± 0.138	2.145 ± 0.162	1.961 ± 0.174
40	2.250 ± 0.115	2.244 ± 0.135	2.236 ± 0.107	2.011 ± 0.183

and 37 μg/L) and tap water (control) for up to 40 d. Resistance to a lethal level of lead was measured in survival-interval tests (SIT) beginning on preexposure days 10, 20, 30, and 40. Changed resistance to lead was assayed by comparing the survival intervals of lead-preexposed fish with those of control fish preexposed to tap water and tested under the same conditions.

Yearling brook trout, 19.2 ± 6.1 g at the outset, were obtained from Merlin Trout Farm, Wentworth, Nova Scotia. They were held in an 1800-L fiberglass tank with a continuous flow of dechlorinated fresh water for 2 mo prior to the experiments. During this period, fish were fed daily with trout pellets at a daily rate of 2.5% of increasing wet body weight. This ration was also fed during the preexposure period but they were not fed during SIT. The test water was dechlorinated Halifax municipal tap water (hardness as $CaCO_3$: 30 mg/L; lead <2.0 μg/L). During the experiments, temperature of the test water was 4.3–8.3°C, pH was 7.6–8.1, and dissolved oxygen was at least 85% of air saturation. Stock solutions of lead were prepared by dissolving crystals of analytical grade lead nitrate in distilled water. Lead analysis for samples from SIT tanks was performed directly by atomic absorption spectrophotometry (AAS) using Perkin–Elmer model 2380 and employing the method recommended by the Perkin–Elmer Corporation (Anonymous 1976). Analysis of lead for samples from preexposure tanks was performed by extraction using the ammonium pyrrolidine dithiocarbamate chelate coprecipitation method described by Boyle and Edmond (1975) and subsequent measurement by AAS.

One week before the start of lead preexposure, four batches of fish were unselectively withdrawn from the stock tank and transferred to four preexposure tanks, 290 fish in each tank. These preexposure tanks (150 L) received test water at 3 L/min. Replacement time for 90% of the test water was calculated to be 1.6 h (Sprague 1969). Fish in these four tanks were acclimated to these conditions for 7 d. Then, the preexposure phase began by supplying three of the four preexposure tanks with lead solutions of 10, 24 and 37 μg/L, respectively; the fourth tank received only dechlorinated tap water for the control group.

After 10, 20, 30, and 40 d of preexposure, 60 fish were drawn from each of these preexposure groups and respectively divided unselectively into six subgroups of 10 and each of these was placed into one of four compartments in each of six SIT tanks (250 L) divided into quadrants by fiberglass screen partitions. The SIT tanks received 2 mg Pb/L solution at 2.5 L/min. Replacement time for 90% of the test water was 1.9 h. Analyses revealed that there were no differences in lead concentration, pH, and dissolved oxygen in various sites in the tank. It was assumed, therefore, that all subgroups were exposed to the same conditions. Mortality observations were made every 8 h from the beginning of the SIT until 100% mortality was reached. Survival interval of each fish was recorded. The criteria for death were the loss of respiratory movements and a failure to respond to mechanical stimulation. Dead fish were removed at each observation.

Survival intervals of individuals were transformed to common logarithms to establish normality before statistical analysis. Two-level nested analysis of variance followed by a Student–Newman–Keul test for comparisons of means were used to analyze the significance of differences in survival intervals among the treatments. All survival interval data complied with statistical requirements of normality (probability plot correlation coefficient test) and homogeneity of variance (Schéffe–Box test).

Results and Discussion

No mortality occurred during the preexposure periods and no behavioral abnormalities were observed. However, different levels of preexposure resulted in significantly different survival intervals in 2 mg Pb/L (Table 1).

Survival intervals of fish preexposed to 10 μg Pb/L were not significantly different from those of the control group at the preexposure interval. Preexposure of fish to 37 μg Pb/L for 10, 20, 30, and 40 d resulted in significantly lower resistance to the lethal lead exposure compared with that of the control ($P < 0.01$). Fish preexposed to 24 μg Pb/L displayed a changing response in their survival intervals in subsequent lethal lead exposure. After 10 and 20 d of preexposure, the survival intervals of these fish significantly decreased in subsequent SIT compared with that of the control ($P < 0.05$). However, their survival intervals became statistically indistinguishable from that of the control and significantly longer ($P < 0.01$) than that of 37 μg Pb/L preexposed fish after 30 and 40 d of preexposure. This changing response suggests that, within the preexposure periods, fish were able to acclimate to such lead (24 μg/L) exposure, by developing some resistance mechanism, as preexposure progressed. After 10 and 20 d of preexposure to 24 μg Pb/L, fish may not have developed the resistance mechanism, or may be in the process of development of this mechanism, which, however, was still not sufficiently able to

withstand the subsequent lethal level of lead. Therefore, as a result, these fish suffered an initial lead sensitization which rendered them less resistant to subsequent lethal exposure. After 30 and 40 d of preexposure, these fish apparently recovered from their initial lead sensitization and became less sensitive to lead compared with control fish. This phenomenon may be considered as acclimation of fish to preexposure of 24 μg Pb/L. The changes in survival interval of lead-preexposed fish may be considered as the result of the interaction between two mechanisms. One is the toxic mechanism and the other is the resistance mechanism. If the former played the main role, the fish would become sensitive to subsequent lead exposure (such as fish preexposed to 37 μg Pb/L for 10–40 d and fish preexposed to 24 μg Pb/L for 10 and 20 d). If the latter played the main role, the fish would become less sensitive to lead as the result of newly developed resistance mechanism (such as fish preexposed to 10 μg Pb/L for 10–40 d and fish preexposed to 24 μg Pb/L for 30 and 40 d.

Although most waters in Canada have lead levels lower than 10 μg/L, lead levels in aquatic ecosystems may not be constant because of variations in the rates of input, dilution, precipitation, and degradation. High lead concentrations may be encountered by fish from substantial accidental release, toxic effluents encountered during migration to spawning grounds, or contaminated meltwater in spring. These might create acute toxicity or reduce resistance to higher levels of lead or other stresses. On the other hand, variable concentration of waterborne lead, uneven distribution of lead, and active swimming ability of fish may give the lead-exposed fish the chance of acclimation and recovery.

The primary use of the data generated by toxicologic tests is their incorporation into safe level recommendations for chemicals entering the aquatic environment. Several sublethal toxicity tests, such as measurement of growth, behavior, and histopathogenesis, have been suggested in the establishment of safe levels. However, some of these methods are variously costly, time consuming, or not sufficiently sensitive. For example, life cycle tests in which fish are exposed to a pollutant for a year or longer are sometimes used to predict safe levels. However, it is impossible to study some important fish in this way, and even if possible, full life-cycle toxicity studies are costly and require long exposure. For example, Holcombe et al. (1976) determined the maximum acceptable toxicant concentration (MATC) to be between 58 and 119 μg Pb/L for brook trout by exposure of three generations to sublethal lead; their experiments lasted for 3.5 yr. Therefore, a short-term indicator of sublethal lead toxicity would provide a faster, more economical way for setting water quality criteria. In the present study, we experimented for only a few weeks and found that brook trout preexposed to 37 μg Pb/L were rendered less resistant to subsequent lethal lead exposure. Our study indicated that the MATC of lead for brook trout should be set between 24 and 37 μg Pb/L.

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Oxygen Conditions in Two Prairie Pothole Lakes During Winter Ice Cover

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Baird, D. J., T. E. Gates, and R. W. Davies. 1987. Oxygen conditions in two prairie pothole lakes during winter ice cover. Can. J. Fish. Aquat. Sci. 44: 1092–1095.

Winter oxygen depletions rates (WODR) from two small southern Alberta prairie lakes were much higher than reported in 1979 for similar lakes in Manitoba. Depletion of oxygen was nonlinear, and the most appropriate regression model used a log transformation indicating that depletion was exponential. A correlation between WODR and sediment organic content was found both within and between the two lakes studied. Spatial variation in WODR indicated that whole-lake WODR based on single-point vertical profiles may be highly inaccurate. Oxygen concentrations in the water column stabilized at low (0.5–2.0 $mg \cdot L^{-1}$) levels although an anoxic water layer may occur over the sediment.

Les taux d'épuisement d'hiver de l'oxygène de deux petits lacs des prairies du sud de l'Alberta étaient de beaucoup supérieurs à ceux signalés en 1979 pour des lacs semblables du Manitoba. L'épuisement de l'oxygène n'était pas linéaire et le modèle de régression le plus approprié comportait une transformation logarithmique, ce qui indique un épuisement exponentiel. Une corrélation entre les taux d'épuisement d'hiver de l'oxygène et la teneur en matières organiques sédimentaires a été notée tant au sein des deux lacs étudiés qu'entre eux. La variation spatiale du taux d'épuisement indiquait que la détermination d'un tel taux à partir de profils verticaux à points uniques pouvait s'avérer très inexacte. Les concentrations d'oxygène dans la colonne d'eau étaient stabilisées à de faibles valeurs (0,5–2,0 $mg \cdot L^{-1}$), mais l'on pouvait noter une couche d'eau anoxique au-dessus des sédiments.

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Differential depth distributions of macroinvertebrates in temperate zone lakes (Davies and Everett 1977; Dall 1979; Boag 1981) may be correlated with species-specific abilities to endure seasonal periods of hypoxia or anoxia. To test such hypotheses, oxygen conditions must be characterized both spatially and temporally.

To date, studies on winter oxygen conditions under ice have been concerned with predicting the rate of oxygen depletion in early winter. A number of models have been proposed which deal with whole-lake oxygen depletion, but in many cases these are based on data from single-point vertical profiles taken in the deepest part of the lake, particularly for small lakes (e.g. Barica and Mathias 1979). More recently, Babin and Prepas (1985), in forwarding a more general model of winter oxygen depletion rates (WODR) for temperate zone lakes, have criticized the single-point profile method and show that, at least in deeper lakes, the concentration of oxygen within horizontal strata at different locations within a lake may be highly heterogenous.

This study describes the oxygen conditions over winter in two ice-covered prairie pothole lakes, both temporally (by continuous monitoring) and spatially (in shallow and deep zones), and therefore presents more detailed information than in previous studies on lakes of this type (Barica and Mathias 1979; Mathias and Barica 1980).

Study Sites

Stephenson's Pond (STP) is a small permanent pothole lake located 15 km northwest of Calgary, with a surface area of 1.93 ha, a mean depth of 1.54 m, and a mean summer conductivity of 450 $\mu S \cdot cm^{-1}$. It is characterized by midsummer blooms of the blue-green alga *Aphanizomenon flos-aquae*. In the summer it has a mean chlorophyll *a* value of 109.3 $\mu g \cdot L^{-1}$, a mean summer total phosphorus (TP) of 1500 $\mu g \cdot L^{-1}$, and a mean winter TP of 1400 $\mu g \cdot L^{-1}$ (method of Menzel and Corwin 1965), indicating that STP is hypereutrophic (Wetzel 1983). Extensive macrophyte beds occur in the littoral zone in summer. The mean summer euphotic zone depth was 1.24 m (the depth to 1% surface irradiance measured with a protomatic photometer).

Pedersen Meadows Pond (PMP), also a pothole lake, is located 1.5 km southeast of STP. Originally a temporary pond, it has been made permanent by the construction of an earth dam at the southeast end. As there is no inflow, PMP can still be considered a true pothole lake. It has a surface area of 2.90

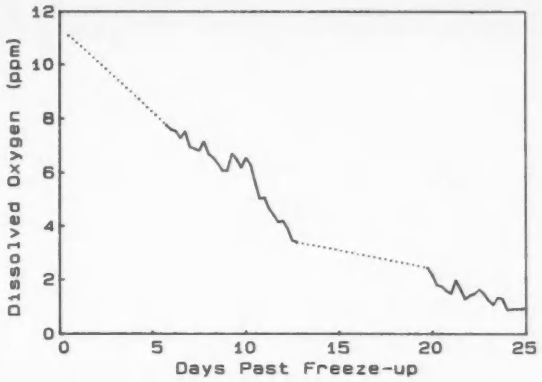

FIG. 1. Changes in dissolved oxygen concentration at the 1-m sonde position (shallow) in Stephenson's Pond in the first 25 d of complete ice cover during the winter of 1984–85.

ha and a mean depth of 2.23 m. Macrophytes occur but not at the densities found in STP. Summer blue-green algal blooms have not been observed.

Materials and Methods

Oxygen readings were taken in both lakes between October 1984 and April 1985. Hydrolab remote datasondes recorded oxygen readings hourly for 2-wk periods each month, 10 cm above the mud in both the shallow and deep zones of each pond (1 and 2.0 m in STP; 1 and 2.8 m in PMP). In addition, two vertical profiles were taken adjacent to the sondes at 0.5-m depth intervals using a YSI oxygen meter. Profiles were also taken at depths of 0.5 and 1.5 m in STP and at depths of 0.5, 1.5, and 2.0 m in PMP to accurately characterize oxygen conditions over the total range of depths in each lake. Both instruments employed Clark-type polarographic cells, which are less sensitive to differences in pH (Legler 1966) and to the occurrence of H_2S than the standard Winkler technique normally employed in such studies (see Madera et al. 1982).

In both lakes, the sediments were mapped by taking 10-cm cores ($n = 63$ in STP; $n = 26$ in PMP) in early March 1985. The cores were oven dried at 50°C for 2 d, weighed, combusted at 550°C for 24 h in a muffle furnace, and organic content calculated as loss of dry weight on ignition (LOI). Oxygen profiles were taken over the location of each core sample to assess the variability in oxygen concentration within each depth zone and its relationship to sediment organic content.

To compare the results from STP and PMP with models used to predict WODR in other lentic systems, the total amount of oxygen present within each lake on different dates was calculated using the techniques of Babin and Prepas (1985). The oxygen concentration in each 0.5-m stratum was multiplied by the stratum volume and the total oxygen mass obtained by summing the totals for all strata. Correction for ice depth, accounting for freeze-out of oxygen, was made by subtracting the volume of ice in each of the upper strata from the total stratum volume to obtain the volume of water in each stratum in the liquid phase containing oxygen (Barica and Mathias 1979; Babin and Prepas 1985). To facilitate comparison of WODR in STP and PMP with those predicted by other models, total lake oxygen mass was expressed on an areal basis (grams of oxygen per square metre) and WODR calculated by the least squares regression of oxygen mass on days past freeze-up over the linear phase of the oxygen depletion process (determined visually), corresponding to a period of 35 d in STP and 42 d in PMP.

To compare oxygen depletion between depth zones, oxygen mass was expressed areally and WODRs obtained by least squares regression. Significant differences between slopes were tested using the *t*-test (Zar 1984). One-tailed *t*-tests were used to compare LOI within lakes. All analyses were performed at the $\alpha = 0.05$ level of probability.

Results

In both lakes, dissolved oxygen concentrations decreased rapidly during the first month following freeze-up (Fig. 1), subsequently reaching low but stable values after 30 and 42 d in STP and PMP, respectively. Isopleth diagrams constructed from vertical profiles taken in the shallow and deep zones in both lakes (Fig. 2) show that oxygen concentrations reached extremely low (but not zero) levels by the end of November. Thus, water in close proximity to the sediment became deoxygenated more rapidly than surface water, confirming that the sediment was the primary site of oxygen uptake, rather than the water column. This validates the use of areal rather than volumetric oxygen mass as the dependent variable in the WODR analyses.

Although H_2S was present in the water from the deeper strata of both lakes throughout the period of winter ice cover, low, but consistent levels of dissolved oxygen were recorded both by the sondes and the YSI meter and confirmed on one occasion using the standard Winkler technique. Benthic samples collected throughout the winter revealed that all the major constituents of the benthic macroinvertebrate community persisted throughout the period of ice cover. One of these species (the leech *Nephelopsis obscura* Verrill) is unable to tolerate complete anoxia for more than 50 d (Davies et al. 1987), persisted for more than 180 d under ice cover, indicating that in STP and PMP, complete winter anoxia does not occur in the water column. Continuous snow cover from October until March ruled out under-ice primary production as a source of oxygen over winter.

In the spring, rapid melting of ice at the margins of both lakes contributed to rapid reoxygenaton. By late April, under-ice primary production resulted in complete reoxygenation of all parts of both lakes, with pronounced levels of hyperoxia in the surface waters (Fig. 2). Hyperoxia is a common phenomenon in pothole lakes in spring (Barica and Mathias 1985).

Untransformed areal WODRs (grams of oxygen per square metre per day) (Table 1) calculated from the linear portion of the WODR curves (Fig. 3) are the highest recorded for pothole lakes (cf. Barica and Mathias 1979: 0.21–0.42 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in Manitoba). WODRs predicted from the models of Barica and Mathias (1979) and Babin and Prepas (1985), which use only mean depth as a predictor, were considerably lower than the observed WODRs in STP and PMP (Table 1). The Babin and Prepas (1985) model, which incorporates a measure of productivity (mean summer TP in the euphotic zone) in addition to mean depth, predicts a much higher (although still underestimated) WODR for STP for which the appropriate productivity data were available (Table 1).

A comparison between the different depth zones within each lake shows clearly that the deep zones depleted more rapidly

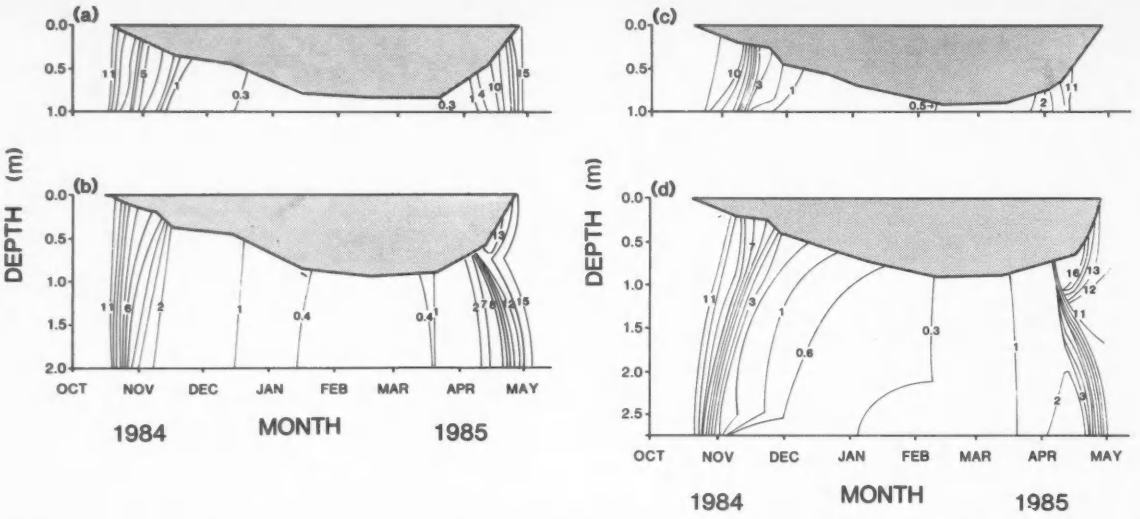

FIG. 2. Depth–time isopleths of oxygen concentration ($mg \cdot L^{-1}$) under ice cover (shaded) in Stephenson's Pond at (a) 1.0 m and (b) 2.0 m and in Pedersen Meadows Pond at (c) 1.0 m and (d) 2.75 m.

TABLE 1. Comparison of observed winter oxygen depletion rates (WODR) ($g\ O_2 \cdot m^{-2} \cdot d^{-1}$) with WODRs predicted by models from Barica and Mathias (1979) and Babin and Prepas (1985) for Stephenson's Pond and Pedersen Meadows Pond.

	WODR	
	Stephenson's	Pedersen Meadows
Observed	0.516	0.617
Barica and Mathias 1979[a]	0.236	0.278
Babin and Prepas 1985[b]	0.227	0.234
Babin and Prepas 1985[c]	0.290	—

[a]$WODR = 0.14 + 0.062\bar{z}$ ($\bar{z}$ = mean depth).
[b]$WODR = 0.214 + 0.0084\bar{z}$.
[c]$WODR = -0.101 + 0.000247TP_{summer} + 0.0134\bar{z}$.

than the shallow zones (STP: $t = 4.12$; PMP: $t = 7.58$) (Table 2). A comparison of the organic content of the sediment from the shallow and deep zones shows that deep zone sediments were significantly higher in organic content than shallow zone sediments based on LOI (STP: $t = 7.18$; PMP: $t = 4.37$, on arcsine transformed data) (Table 2). Thus, there is a relationship between oxygen depletion rate in different depth zones and sediment organic content.

Detailed mapping of the oxygen concentrations at 63 locations in STP and 26 locations in PMP showed that after stabilization, oxygen concentrations with in depth zones were identical for all locations in both lakes.

Discussion

Low, but significant amounts of oxygen in the water column of both STP and PMP over the period of winter ice cover, together with the persistence of a variety of nonencysting macroinvertebrate species, show that in southern Alberta, pothole lakes that do not freeze all the way to the sediment are probably not completely anoxic over the winter period, although an anoxic water layer may occur over the sediments.

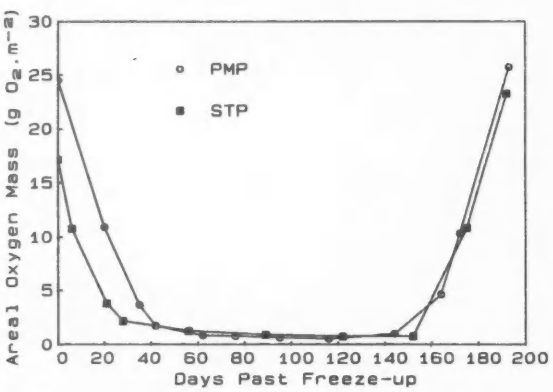

FIG. 3. Changes in areal oxygen mass ($g\ O_2 \cdot m^{-2}$ exposed surface area) under ice cover in Stephenson's Pond (STP) and Pedersen Meadows Pond (PMP) during the winter of 1984–85.

This was true, despite the fact that during the initial stages of winter oxygen depletion in both STP and PMP, the rate was more rapid than reported for pothole lakes in previous studies (Barica and Mathias 1979). The fact that oxygen did not become totally depleted in the water column indicates that after its initially rapid rate, WODR slows down, suggesting that WODR might better be modelled as a nonlinear process, as suggested by Babin and Prepas (1985). The rate of oxygen depletion can be considered a function of the metabolic rate of the sediment and the rate of oxygen supplied to the sediments through eddy diffusion (Babin and Prepas 1985). Since both of these factors are to a large extent governed by temperature, it is pertinent to note that the period of rapid depletion observed in PMP and STP also coincided with the period of thermal equilibration between the sediment and the overlying water column (unpublished data). There is a need for a more detailed study of

TABLE 2. Winter oxygen depletion rates (WODR) (g $O_2 \cdot m^{-2} \cdot d^{-1}$) in Stephenson's Pond and Pedersen Meadows Pond with coefficient of determination (r^2) and corresponding analysis of sediment organic content by percent loss of dry weight on ignition (% LOI). Shallow = shallow zone; deep = deepest zone of lake; n = sample size; SE = standard error.

		WODR	r^2	% LOI	n	SE
Stepehenson's	Shallow	0.337	0.96	11.44	20	0.78
	Deep	0.679	0.94	18.58	43	0.48
Pedersen Meadows	Shallow	0.249	0.96	9.65	11	0.94
	Deep	0.672	0.98	14.61	15	0.59

the interaction between these factors if an accurate description of the processes which govern winter oxygen depletion are to be obtained. However, there is no doubt that lake productivity (in terms of summer primary production and nutrient levels and organic content of the sediments) is an important factor governing the rate of winter oxygen depletion and must be incorporated into WODR models, as shown by Babin and Prepas (1985).

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LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Trophic Relationships in Freshwater Pelagic Ecosystems: A Question of Averages and Sampling Error?

In their investigation, McQueen et al. (1986) set out to determine whether resource limitation or consumer control ultimately determines the maximum biomass of different trophic levels. They conclude that (1) maximum biomass at each trophic level is controlled from below (bottom-up) by nutrient availability rather than controlled from above (top-down) by consumers, (2) this bottom up regulation weakens at each succeeding step up the food web, and (3) variability around the bottom-up relationships can be explained by top-down forces. Because many researchers have tried to determine how the maximum biomass of different trophic levels is determined, the study deserves attention and the results require careful interpretation.

A key aspect of the concept of population regulation, which McQueen et al. (1986) do not specifically define in their paper, involves the belief that "some factor(s) must actively operate to keep the numbers of animals within certain predetermined bounds, or return them to some predetermined mean density" (White 1978) (i.e some equilibrium level). I will argue below that (1) the premise for McQueen et al.'s (1986) study is based on improper comparisons of predator–prey relationships obtained from studies which study different aspects of ecosystem dynamics and (2) the weakening of bottom-up relationships as one moves towards higher trophic levels may be entirely an artifact of sampling error rather than an effect of top-down forces.

(1) McQueen et al.'s (1986) separation of predator–prey relationships into bottom-up and top-down categories represents the separation of data obtained from different survey and experimental designs. The first category, referred to as bottom-up relationships, is a representation of mean annual conditions estimated from a large number of samples taken throughout the productive season and representing an average over the seasonal cycle centered on an equilibrium point (e.g. McCauley and Kalff 1981; Hanson and Peters 1984). The second category, referred to as top-down, represents repeated measurements of "biomanipulations" in which the development of different trophic levels is monitored starting from a variety of different initial conditions, over periods of days, weeks, or at most a few months. However, measurements from such biomanipulations do not represent the average of a seasonal cycle around an equilibrium point. Instead, it would appear that McQueen et al. (1986) are comparing (a) relationships between the equilibrium point of two adjacent trophic levels to (b) the population trajectories leading towards, but not necessarily reaching, the equilibrium levels. This means, for example, that the results from McQueen et al.'s enclosure experiments should not be represented as fitted regressions of the abundance of one trophic level as a function of the abundance of another but rather by fitting time-dependent population cycles. It is well established that only by contrasting averages taken over a suitable period, relative to the population cycle or the generation length of the organism under investigation, can relationships between predator–prey abundance establish accurate equilibrium biomass levels (Bendat and Piersol 1966).

(2) Consumers certainly may influence their food resources. Furthermore, oscillations of multispecies assemblages and their equilibrium point are dependent on the relative position of organisms along a food chain as well as their intrinsic growth rates (May 1973; Tanner 1975). Nonetheless, the claim by McQueen et al. (1986) that bottom-up regression based relationships diminish in relative strength up the food web is not necessarily correct. The diminishing strengths may in fact reflect two types of measurement error.

The first type may be due to estimating the mean equilibrium abundance of a trophic level over too short a time period relative to typical life cycles of taxa at that level. For example, fish populations generally consist of several age-classes and can fluctuate on time scales of several years. Thus, estimating mean equilibrium abundance using only a few years of data may be misleading if the population is either at a high or low point in its cycle. If populations from different sites are fluctuating out of phase, then additional error would be introduced into any relationship derived from the data.

The second type of error in estimating the average abundance of a trophic level may be due to the increasing difficulty and cost of taking comparable numbers of samples with comparable accuracies as size of the organism increases. The estimated variance of a variable will decrease as an inverse function of sample size (Sokal and Rohlf 1969, p. 133). In the studies cited by McQueen et al. (1986), the mean for each trophic level in each location is estimated from fewer samples as one moves up the food web. Estimates of mean phosphorus, phytoplankton, and zooplankton concentration were based largely on weekly and biweekly samples (McCauley and Kalff 1981; Hanson and Peters 1984), while those estimating fish biomass are based on fewer samples much more widely spaced (Hanson and Leggett 1982; Mills and Schiavone 1982). Although replicate samples at lower trophic levels might be more variable than replicate samples at higher trophic levels, the trade-off of variation among replicates versus sample size must be determined empirically before any conclusion about relative variation at different trophic levels can be made. Furthermore, it is important to note that sampling frequency and the time interval between the sampling of different lakes may also influence the variance in the estimates of population abundance for different types of organisms.

To illustrate the potential significance of error due to differences in the number of samples taken to estimate the abundance of different trophic levels, I carried out a simulation study in which the means for two variables were estimated for 25 cases (sites). The two variables were assumed to have a 1:1 log–log relationship. The mean for each site and variable was

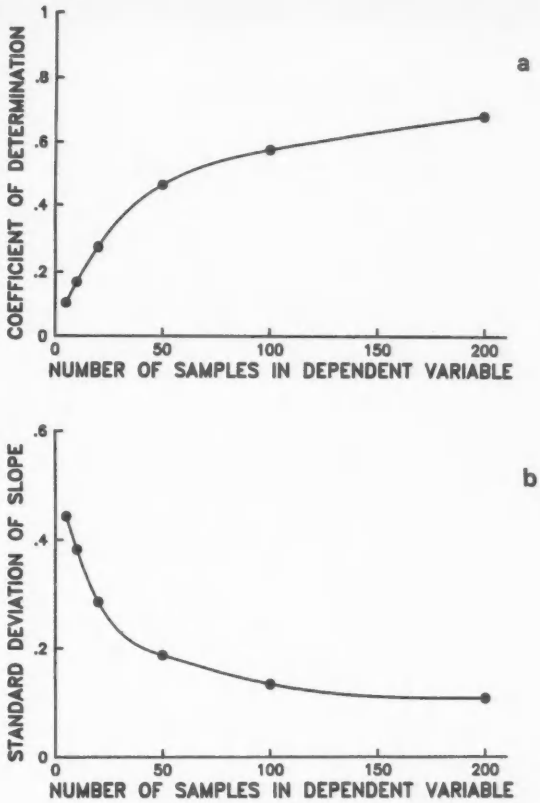

FIG. 1. Plots of the (a) coefficient of determination and (b) standard deviation of the estimated slope as a function of the number of samples used to calculate the mean of the dependent variable for each case used to establish a linear relationship between dependent and independent variables. The mean for the independent variable was estimated from 200 samples. The points on the figure represent the average values obtained from 250 simulations.

estimated from repeated sampling assuming a log-normal error distribution ($X = xe^{\epsilon}$, where x is the true mean, $E(\epsilon) = 0$, and var $(\epsilon) = \sigma^2 = 1$). The sample size used to estimate the mean of the independent variable for each site was set at 200. The sample size used to estimate the mean of the dependent variable at each site was varied from 5 to 200. The regression and correlation coefficients were calculated using the 25 pairs of observations. The simulation was repeated 250 times. Figure 1a shows that as the number of samples in the dependent variable drops below 100, the mean coefficient of determination (r^2) drops sharply. Simultaneously, the standard deviation of the slope (based on 250 estimates) increases sharply (Fig. 1b). Thus, as the sampling of one of the populations becomes increasingly difficult, the error associated with an empirical relationship will also increase.

In order to make any interpretation about causal links based on regressions between the abundance of organisms at different trophic levels, it is necessary to document the comparability of the estimates used to derive these relationships. Furthermore, to properly understand which factors determine equilibrium biomass levels throughout a food chain, investigators must consider the rates at which organisms at succeeding trophic levels can feed, grow, and reproduce — Pierre Pepin, *Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, Nfld. A1C 5X1.* (J8996)

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Reply to Pierre Pepin

We would like to thank Dr. Pepin for the interest he has taken in our paper (McQueen et al. 1986). Dr. Pepin has raised three concerns and we are pleased to have this opportunity to reply. Pepin argues that (1) McQueen et al. (1986) is based on "improper comparisons of predator–prey relationships obtained from studies which study different aspects of ecosystem dynamics" and (2) the observed weakening of bottom-up relationships from the bottom to the top of the food web "may be entirely an artifact of sampling error" due to variation in sample size and (3) due to variation in life cycles of organisms at different trophic levels.

We explicitly stated that our presentation of bottom-up and top-down relationships "are supported by two very different data sets" (McQueen et al. 1986, p. 1575). Pepin is certainly correct to mention that they represent "different aspects of ecosystem dynamics." The bottom-up regressions that we presented in fig. 4 (McQueen et al. 1986) represent the mean relationship between adjacent trophic levels composed of various interyear and interlake data sets from the published literature. The top-down relationships represent the impact of variation in predator abundance on prey abundance. Examination of the data derived from nine enclosure experiments (McQueen et al. 1986; McQueen and Post 1984; Post 1984) shows that the observed effect of variation in predator abundance on prey abundance is not a seasonal effect. The top-down regressions do not represent "time-dependent population cycles" as suggested by Pepin, but rather quantify the relationships between

predator and prey abundance independent of time. The hypothesis that we proposed in McQueen et al. (1986) was that the large variation observed in mean bottom-up regressions derived from the published literature could be explained by variation in predation pressure at higher trophic levels. We suggest that our comparison between the bottom-up and top-down data sets is appropriate because our hypothesis is that top-down regulation is the mechanism that may explain the observed variation in relationships between lower adjacent trophic levels. Furthermore, we hypothesized that these predator impacts would be stronger at the top of the food web than at the bottom. This view of pelagic food web structure implies that (1) maximum potential biomass is determined by the availability of nutrients through bottom-up relationships and (2) realized biomasses (as represented by the bottom-up regressions in the literature) are seldom or never at equilibrium, but are constantly shifting in response to changes in both bottom-up and top-down impacts. Our analysis suggested that variation in predator abundance (within naturally occuring ranges) was sufficient to explain the variation about the observed realized biomasses in the literature bottom-up regressions.

The second concern raised by Dr. Pepin deals with the statistical validity of our conclusion that the coefficient of determination (r^2) (table 2, McQueen et al. 1986) is higher near the bottom of the food web and lower near the top. Dr. Pepin argues that this could be simply due to differences in sample size. On purely statistical grounds, his argument is correct, but it is not supported by the available empirical limnological literature. Examination of the sample sizes and coefficients of determination from literature bottom-up regressions, presented in table 2 (McQueen et al. 1986), refutes Pepin's assertion that our conclusions were inappropriate. There is no apparent relationship between sample size (range in $n = 10$ to 207) and coefficient of determination in the empirically determined data. With small sample size ($n = 10$ to 13), coefficients of determination are highest at the bottom of the food web and decrease at higher trophic levels (phosphorous versus phytoplankton $r^2 = 0.93, 0.81$; phytoplankton versus zooplankton $r^2 = 0.81, 0.377$; zooplankton versus planktivores $r^2 = 0.24, 0.08$). With large sample size ($n > 100$), the same pattern of decreasing coefficients of determination at higher trophic levels is apparent in the literature data (phosphorous versus phytoplankton $r^2 = 0.77$; phytoplankton versus zooplankton $r^2 = 0.63, 0.43$). We therefore suggest that the combined coefficients of determination we presented in McQueen et al. (1986) (phosphorous versus phytoplankton $r^2 = 0.81$; phytoplankton versus zooplankton $r^2 = 0.58$; zooplankton versus planktivores $r^2 = 0.16$) best represent the available data. Further verification of this conclusion awaits publication of additional data sets, particularly at the higher trophic levels.

The final concern raised by Dr. Pepin is that the organisms found at each trophic level have very different life cycles: "Thus, estimating mean equilibrium abundance using only a few years of data may be misleading if the population is either at a high or low point in its cycle." It is these interannual variations in piscivorous and planktivorous fish abundance that have been hypothesized to cascade through lower trophic levels (Carpenter et al. 1985). If the hypotheses that we have proposed (McQueen et al. 1986) withstand the rigors of future scientific investigation, we may find that life cycle times and population response times will prove to be important causal mechanisms. We would predict that at the top of the food web, perturbations that influence fish year-class strength will have large and long lasting impacts which will cascade down the food web. These impacts will have large biomass impacts at the top of the food web where fixed and long life cycles will prevent rapid compensatory responses. However, lower in the food web, at the zooplankton and phytoplankton levels, high species diversity, variable life cycles, and rapid response times might be expected to buffer top-down effects.

In McQueen et al. (1986) we concluded that (1) maximum biomass at each trophic level is controlled by nutrient availability (bottom-up effects), (2) this bottom-up regulation weakens with each additional trophic level, (3) the realized biomass observed in nature is a function of bottom-up effects as modified by predation or top-down effects, and (4) the impact of top-down effects will weaken with each succeeding step down the food web. We suggest that these conclusions are not simply "a question of averages and sampling error" but are strongly supported by the published empirical literature —

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